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A TREATISE ON ZOOLOGY

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PART IV

THE PLATYHELMIA, MESOZOA, AND NEMERTINI

BY

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EDITOR'S PREFACE

THE present volume is the "Fourth Part" in order of a comprehensive treatise on Zoology, which has been for some time in preparation under my editorship. In this treatise each of the larger groups of the Animal Kingdom is to be described by a separate author; whilst, as far as possible, uniformity in method and scope of treatment is aimed at. The authors are, for the most part, graduates of the University of Oxford, though it may not be possible to maintain this limitation in future sections of the work.

The general aim of the treatise is to give a systematic exposition of the characters of the classes and orders of the Animal Kingdom, with a citation in due place of the families and chief genera included in the groups discussed. The work is addressed to the serious student of Zoology. To a large extent the illustrations are original. A main purpose of the Editor has been that the work shall be an independent and trustworthy presentation, by means of the systematic survey, or taxonomic method, of the main facts and conclusions of Zoology, or, to speak more precisely, of Animal Morphography.

The treatise will be completed in ten parts of about the same size as the present one. It will at once be apparent that this limitation necessitates brevity in treatment which, however, will not, it is believed, be found inconsistent with the fulfilment of the scope proposed or with the utility of the work

to students. The immediate publication of the following parts may be expected:—

Part I. Introduction and the Protozoa.

Part II. Enterocœla and the Cœlomocœla—The Porifera — The Hydromedusae — The Scyphomedusae—The Anthozoa—The Ctenophora (published in September 1900).

Part III. The Echinoderma (published in March 1900).

Part IV. The Mesozoa—The Platyhelmia—The Nemertini (the present volume).

These parts will be issued, without reference to logical sequence, as soon as they are ready for the press. This procedure to some extent evades the injustice of making an author, whose work is finished, wait for publication until other more tardy writers have completed their tasks.

The following authors have undertaken portions of the work:—Professor Weldon, F.R.S., M.A. Oxon.; Professor Benham, D.Sc., M.A. Oxon.; Mr. G. C. Bourne, M.A. Oxon.; Mr. G. H. Fowler, M.A. Oxon.; Professor Minchin, M.A. Oxon.; Mr. F. A. Bather, M.A. Oxon.; Professor J. W. Gregory, D.Sc.; Mr. E. S. Goodrich, M.A. Oxon.; Professor Hickson, F.R.S. of Manchester; Mr. J. J. Lister, F.R.S., M.A. Cantab.; Mr. Arthur Willey, D.Sc.; Professor Farmer, F.R.S., M.A. Oxon.; Mr. R. I. Pocock; and Mr. Martin Woodward.

E. RAY LANKESTER.

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NOTE

It is but just to the author to put on record the fact that the MS. of the chapters on the Platyhelmia were written during the years 1895-97; much of it was printed, and the proofs corrected in 1897; and the whole of the Part was in proof, and most of the figures were already prepared, early in 1898, when the author left England for New Zealand. At the same time the editor is satisfied that no important omissions due to this fact occur in the book, the proofs of which have been revised and some additions made during the present year.

E. R. L.

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APPENDICES TO PHYLUM.

Rhombozoa, Orthonectida, Trichoplax, etc.

[1] Phylum Platyhelmia, Lankester, 1890 (*Platyelmia*, Vogt, 1851; *Platodes*, Leuckart, 1854; *Platyelminthes*, Gegenbaur, 1859; *Plathelminthes*, Minot, 1877).

THE group of "Flatworms" constitutes one of the phyla of the Metazoa. Linnaeus associated *Lumbricus* with the various worms which are now known as Flukes, Tapeworms, Nemertines, Nematodes, and Leeches in the order "Intestina," which he placed close to his heterogeneous group "Mollusca," in a class "Vermes."

Lamarck separated the parasitic worms, for which he retained the term "Vermes," as a class distinct from the Chaetopodous worms, to which he gave the name "Annélides." Lamarck's "Vermes" is thus essentially synonymous with the "Entozoa" of various subsequent writers. And in spite of the fact that as long ago as 1850 Grube[1] pointed out the affinities of the Annelids with the Arthropoda, and insisted upon the unnatural character of "Vermes" as a group, and although Lankester[2] was one of the earliest of the more recent zoologists to give up the term "Vermes," and the truth of this view has become more and more evident in recent years, yet many writers still retain this name almost in the sense of Linnaeus. Leuckart[3] in 1848 broke up the "entozoic worms," and associated the Cestodes with the Acanthocephala as "anenterous worms," which he separated from the "apodous worms" (Turbellarians, Trematodes, and Leeches); while the other parasitic forms (Nematodes) were recognised as distinct from these and placed with the Annelids. Later on, however, he[4] put the Cestodes in a more natural position, in a group "Platodes," which included the Trematodes, Turbellaria, Nemertines, and Leeches.

But Vogt[5] had already recognised in 1851 the affinity of these various worms and invented the term *Platyelmia* for the group, in the sense in which it is usually understood at the present time. The name was modified by Gegenbaur[6] to Platyelminthes, and adopted by Carus, Schneider, Haeckel, and others; Haeckel in 1877 removed the Nemertines from the Platyelminthes (to which group, however, he gave the name "Acoelomi") and placed them with the rest of the "Vermes" as "Coelomati." Lankester[7] modified Vogt's terminology and still retained in his "Platyhelmia" the Nemertina and Hirudinea But recent researches on the anatomy and development of the latter class, and amongst others, Burger's work on the Nemertines, have shown conclusively the necessity of removing them from the neighbourhood of the Flukes,

[1] Grube, *Die Fam. d. Anneliden*, *Arch f. Naturgesch* 16 1850, p. 249.
[2] Lankester, *Notes on Embryology and Classification*, 1877
[3] Leuckart, *Ub. Morphol. u. Verwandsch d Wirbellose Thiere*, 1848
[4] Leuckart, *Arch. f. Naturgesch. Jahrg.* 20 1854.
[5] Vogt, *Zoolog. Briefe*, 1851, vol. i. p. 185.
[6] Gegenbaur, *Die Grundzuge d. Zoologie*, 1859
[7] Lankester, *The Advancement of Science*, 1890, and *Encycl. Brit.* ix. edit., art. "Zoology."

Tapeworms, and Turbellarians, which alone are now included amongst the Platyhelmia, together with the probably degenerate forms known as "Mesozoa."

The Characters of the Platyhelmia.—The animals belonging to the three classes—Turbellaria, Trematoda, and Cestoidea—while exhibiting many differences in form, habits, and life-history yet present certain fundamental points of agreement, so that it is possible to picture a common ancestor from which the three groups have been descended. Such an ideal Platyhelminth would have had a somewhat oval body, flattened from above downwards, and with a distinct prostomium or region in front of the mouth and containing the brain (Fig. II.). The surface of the body was probably clothed with a ciliated epidermis similar to that of the Turbellaria but of a simpler character, so that the animal was able to move freely in the sea; in this movement it was aided by the muscular system which had developed below the epidermis with which it had lost its connection and become arranged to form circular and longitudinal sheets. No doubt the ancestral form was more or less closely connected with the Coelentera by means of animals of which we know nothing (There are some features of resemblance to the Ctenophora, as Lang has pointed out.[1]) But in the Platyhelminth the endoderm had become separated from the ectoderm by a great development of mesodermal tissue filling up the blastocoele, and consisting of vertically arranged muscle cells and of a packing of peculiar connective tissue cells; in this compact mass of cells or parenchyma distinct generative and excretory organs had become differentiated, having each its own independent communication with the exterior. Nevertheless, no definite space, or coelom, existed in the substance of this intermediate mass of cells. The archenteron of the coelenterate ancestor had, however, become separated into a metenteron and a coelom, which is represented by the cavity of the genital organs.

The excretory system consisted of a pair of laterally placed canals, consisting of a series of perforated cells, some of which carry cilia, from each canal small lateral branches are given off which branch and anastomose to form a network from which arise still finer twigs, each of which terminates in a "flame cell" (Fig. I.). This flame cell (or pronephridiostome of Vejdovsky) is a comparatively large, hollow cell from whose base, in which the nucleus is situated, a bunch of long cilia projects into the cavity; the flickering appearance of a flame results from the synchronised movement of the cilia. The cavity of this terminal cell communicates only with the excretory tubule. It is possible that in the earliest ancestors a number of isolated cells became hollowed out, and ciliated like this flame cell,

[1] This is discussed by Mr. Bourne in Part II. "The Ctenophora," pp. 16 *et seq.*

and that each became elongated and effected a communication with the exterior, and it has even been suggested that such cells are derived from unicellular epidermal glands which have gradually sunk into the parenchyma, retaining their communication with the exterior (on the other hand, similar flame cells have been noted amongst the intestinal epithelium). As these isolated cells became more numerous, with the increase in the size of the animal there would be, as in other analogous instances, a tendency to form a common collecting canal which would then replace the numerous

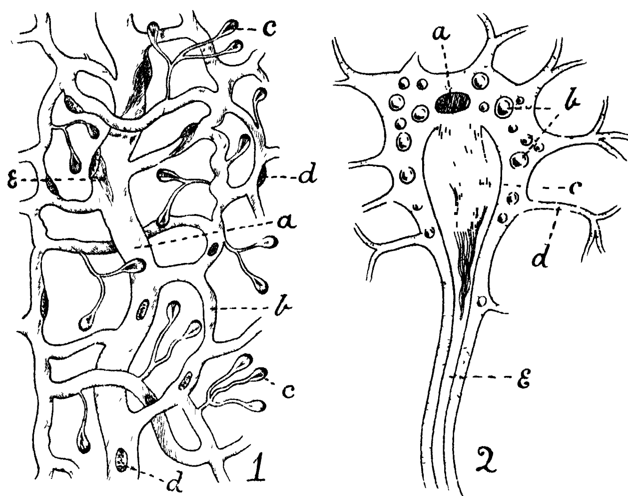


FIG I —Diagram of the Structure of the Platyhelminth Excretory System

1 —A portion of the system of canals *a*, the main canal or duct, receiving numerous secondary canals (*b*); c, flame cells or terminal cells of the capillary vessels, *d*, nucleus in the wall of the canals, *e*, tuft of cilia or "flame," arising from the side of the canal, in the neighbourhood of a nucleus

2.—A flame cell (somewhat diagrammatic) *a*, nucleus, *b*, excretory globules in the cytoplasm, c, the "flame", *d*, protoplasmic processes of the cell which extend amongst the parenchymal cells, and are possibly in connection therewith, *e*, the canaliculated portion of the cell which communicates with the neighbouring excretory tubules

isolated apertures. Nevertheless, in many existing forms, such scattered or regularly arranged, isolated apertures exist either in the absence of, or in addition to, the collecting canal and its pore.

The metenteron was a simple sac, having a single opening to the exterior, which served both for inception of food and ejection of faeces. This mouth was probably somewhere between the centre and the anterior end of the oval body, as it is in many of the Turbellaria. The surface in which the mouth is situated is the ventral surface (Fig. II.).

The nervous system, like the muscular, had separated from the epidermis and had taken on a much more definite form than in the

Coelentera, for the greater number of nerve cells became aggregated near that end of the body which is directed forwards during movement to form a bilobed cerebral ganglion, lying near the dorsal surface, anterior to the mouth, *i.e.* in the prostomium. From it a network of nerve fibres spread in all directions; but certain of these strands of fibres became more important than others; a pair of ventral, a pair of lateral, a pair of dorsal, as well as anteriorly directed nerves were thus distinguishable (Fig. II. 2, 4). But

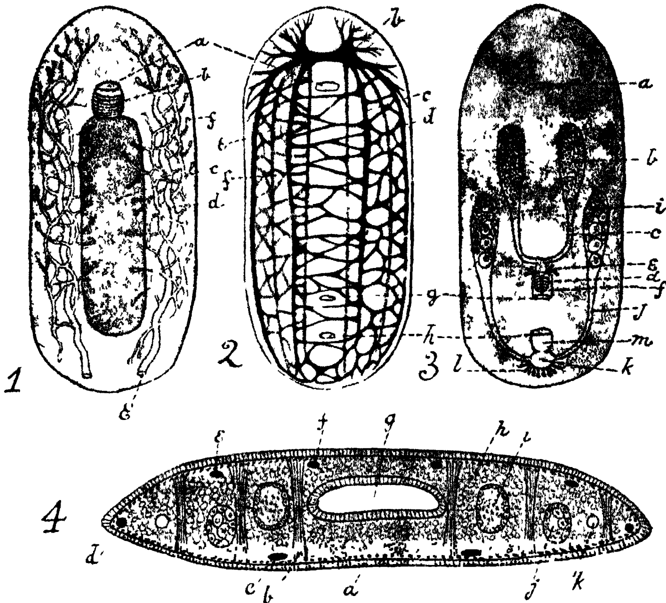


FIG II.—The Anatomy of an Ideal Platyhelminth.

1.—The alimentary and excretory systems. *a*, mouth; *b*, pharynx; *c*, intestine; *d*, main excretory canals; *e*, excretory pore; *f*, flame cells.

2.—The nervous system, ventral view. *b*, cerebral ganglion; *c*, ventral nerve tract; *d*, marginal or lateral nerve tract; *e*, dorso-lateral tract; *f*, medio-dorsal tract; *g*, male genital pore; *h*, female pore.

3.—The reproductive system. *b*, testis; *c*, sperm duct; *d*, penis; *e*, prostate glands opening into the lower part of the sperm duct; *f*, antrum masculinum, in which the penis lies; *g*, male pore; *h*, female pore; *i*, ovary; *j*, oviduct; *k*, spermatheca or dilatation at the junction of the two oviducts; *l*, shell gland opening into this dilatation; *m*, antrum femininum.

4.—A transverse section through the body. *a*, epidermis, below which is seen the layer of circular muscles, represented by the continuous line; below this, the layer of longitudinal muscles, by a series of dots; *b*, vertical, dorso-ventral muscles; *c*, ventral nerve tract; *d*, marginal tract; *e*, latero-dorsal nerve tract; *f*, medio-dorsal tract; *g*, intestine; *h*, parenchyma (mesenchyme); *i*, testis; *j*, ovary; *k*, main excretory canal or duct.

the nerve cells still retain a scattered arrangement, remaining at various points of the general plexus, and do not give rise to ganglia other than the brain. Sense organs were probably represented by patches of pigment in the near neighbourhood of the brain, and of widely distributed sensory cells.

All existing Platyhelmia, with a very few exceptions, are hermaphrodite, and we are justified in attributing to the ancestor a similar character. The male organs consisted of a pair of tubular testes and of ducts, which unite posteriorly to form a muscular copulatory organ capable of being protruded from a median pore behind the mouth. Probably this penis was used for perforating the soft body of another animal at any point, so that special female receptive ducts were not at first necessary.[1] The female system consisted of masses of germ cells, derived from the wall of the archenteron; but very early in the history of this group definite tubular ovaries, the walls of which are produced into special oviducts, were developed, for the liberation of the fertilised ova; these ducts then united to form a special sac for the reception of the penis (*bursa copulatrix*), while other parts of the duct became dilated to form a spermatheca (Fig. II. 3).

Of the descendants of this ideal ancestral Platyhelminth, some have retained the ciliated epidermis and the free mode of life; while others have taken to a parasitic habit, and lose this ciliated covering in the course of their developmental history, and are covered by a "cuticle" in the adult stage; in connection with their parasitism special organs of fixation, suckers and hooklets, are developed in various parts of the body. The line of descent of the free-living forms includes the Turbellaria and the Temnocephaloidea. The parasitic forms embrace two classes—the Trematoda and Cestoidea; in the former the alimentary tract of the ancestor is retained, while in the latter it has been entirely lost, and no trace of it is presented at any period of the developmental history.

CLASS I TURBELLARIA (EHRB.)

Order 1. **Rhabdocoelida.**

Sub-Order 1 **Rhabdocoela.**
Fam. 1 Macrostomidae
" 2 Microstomidae.
" 3. Prorhynchidae.
" 4. Mesostomidae.
" 5. Proboscidae
" 6. Vorticidae.
" 7. Solenopharyngidae.

Sub-Order 2. **Alloiocoela.**
Fam. 1. Plagiostomidae.
" 2. Monotidae.
" 3. Bothrioplanidae.

[1] Cf. Whitman, *Journ. Morph.* iv. 1891, p. 386.

Sub-Order 3. **Acoela.**
Fam. 1. Proporidae.
„ 2. Aphanostomidae.

Order 2. **Tricladida.**
Fam. 1. Otoplanidae.
„ 2. Procerotidae.
„ 3. Bdelluridae.
„ 4. Planariidae.
„ 5. Leimacopsidae.
„ 6. Geoplanidae.
„ 7. Bipaliidae.
„ 8. Cotyloplanidae.
„ 9. Rhynchodemidae.

Order 3. **Polycladida.**
Fam. 1. Planoceridae.
„ 2. Leptoplanidae.
„ 3. Polypostiidae.
„ 4. Cestoplanidae.
„ 5. Anonymidae.
„ 6 Pseudoceridae.
„ 7. Euryleptidae.
„ 8 Enantiidae.
„ 9. Prosthiostomidae.
„ 10. Diplopharyngeatidae

The Turbellaria are Platyhelmia, with a ciliated epidermis, in which the body is nearly always flattened, oval, or leaf-shaped. In the epidermis special cells occur, which may give rise either to mucus, or to granular rod-like bodies, or to definite "rhabdites," which are discharged from the body on irritation.

Historical.—The name "Planaria" was given by O. F. Müller in 1776 to certain worms living in fresh and salt water, and characterised by a leaf-like form, which had previously been confused with a Fluke and a Tapeworm under Linnaeus's name "Fasciola"; later, Muller's genus *Planaria* (which included some Nemertines) was split up into numerous genera, and the genus *Planaria* restricted to certain fresh-water forms; but it has also been employed by several authorities as the name of the class. The name "*Turbellaria*" was invented by Ehrenberg in 1831 to include not only "Planarians," but also the elongated Nemertine worms, which, by means of cilia borne by the epidermis, produce the well-known movement of small particles coming within their reach, giving rise to the appearance of a whirlpool.

Cuvier (1817) was the first to separate his genus *Nemertes* (representing the Nemertines) from *Planaria*, and formed the

orders "Vers cavitaires" and "Vers parenchymateux" for the two groups.

To Ehrenberg, too, we owe the first definite attempt to classify the Turbellaria in the restricted sense; and, indeed, he laid the foundation for all the later systems of the class. He formed two orders—the "Dendrocoela" and "Rhabdocoela" in reference to the character of the intestine.

The next step in classification was made in 1844 by Oersted, who divided the Dendrocoela into two families—(1) marine forms, with short, folded pharynx and very much branched intestine; for them he used the term "Cryptocoela"; and (2) fresh-water forms, with long, tubular pharynx and feebly branched caeca, for which he retained Ehrenberg's term "Dendrocoela."

A fourth group was erected by Uljanin (1870) for gutless forms like *Convoluta*, for which he suggested the term "Acoela," as opposed to the remainder of the Turbellaria, for which he proposed the name "Coelata" (58).

Our present classification is due partly to v. Graff (22), who made a third group in the Rhabdocoela, viz. the Alloiocoela; and partly to Lang (42), who suggested the terms Polyclada for marine, and Triclada for fresh-water and terrestrial Dendrocoeles.

Dreparnaud (1803) may be referred to for his peculiar views on the relationship of the Turbellaria, he regarded them as intermediate between the Mollusca and Annelida; and Oersted held a similar view, that the "Cryptocoela" (Polyclads) or "Planaria molluscina" form a passage to the opisthobranch mollusca. Girard and v. Jhering held somewhat similar views.

Amongst the more important additions to our knowledge of fauna, as well as of general anatomy, the following authors deserve mention:—O. F. Muller (1773-83), who gives recognisable figures and diagnoses of the many new forms discovered by him; O. Fabricius (1820-26), Dugès (1828-32), Ehrenberg (1831-36), Oersted (1844), O. Schmidt (54), and in more recent times, Jensen (35). Moseley's (1874) valuable account of terrestrial Triclads, v. Graff's extensive series of papers and his great monograph on Rhabdocoelida, and Lang's valuable monograph on the Polyclads, form together the best general account of the group. For an account of British marine forms, see Gamble (18).

The anatomy of these worms was first seriously studied by v. Baer in 1827, who dealt with fresh-water Triclads; he was followed by Dugès (15) for Rhabdocoels; by Mertens (1833) for Polyclads; while Quatrefages (1845) gives an excellent account, with very good figures, of the anatomy of various Polyclads. These zoologists may be said to have laid the foundation of our knowledge of the anatomy of the Turbellaria, more especially of the generative organs, which are of so much importance in

classification. Coming to nearer times, the works of Moseley (47), Böhmig (5), Ijima (34), and Vejdovsky (59) will always be conspicuous for the elaborate and detailed account of the structure of various members of the group.

As is frequently the case, the study of the habits—the Bionomics—of the group was begun early, and the observations of some of the older authors still retain considerable value, especially those of O. F. Müller, Bosc (1801), Dalyell (1814-53), J. R. Johnson (36), M. Faraday (16), on the subject of regeneration and asexual reproduction of Rhabdocoels; while F. Schulze (53) and C. Darwin (11) give accounts of general physiology and habits respectively.

Classification of the Turbellaria.—The class is divided into three orders, primarily distinguished by the form of the intestine, viz.—Rhabdocoelida, Tricladida, and Polycladida.

ORDER 1. **Rhabdocoelida**, v. Graff

Turbellaria, in which the intestine is a simple, unbranched sac, which may have ill-defined lobes, or the cells of the intestinal wall may, in degenerate forms, give rise to a syncytium which blocks up the cavity. The female gonads are compact, and generally a pair of germaria and vitellaria. (For an account of this order, see especially 22 and 59.)

SUB-ORDER 1. RHABDOCOELA, Ehrb Rhabdocoelida, in which the intestine is a simple, straight sac; variable pharynx; testes compact; female gonads variable; usually without otolith.

A. Without accessory female copulatory organs FAMILY 1. MACROSTOMIDAE. Ed. v. Ben. The female gonad is an ovary; the female pore in front of the male pore *Macrostoma*, E. v B (Fig. III. 2), *M. Lemanus*, Dupl., is lacustrine; *Omalostoma*, E v B.; *Mecynostoma*, E. v B. FAMILY 2 MICROSTOMIDAE, O. Schm. A pair of ovaries present; asexual reproduction as well as sexual. *Microstoma*, O Schm. (sexes said to be distinct); *Stenostoma*, O. Schmidt; both have ciliated pits (see 49); *Alaurina*, Busch. FAMILY 3 PRORHYNCHIDAE, Diesing. The male pore opens in common with the pharynx; female pore ventral. The female gonad is a single germ-vitellarium. *Prorhynchus*, M. Schm. (see v. Kennel, 39), (Fig III 4, 5). B. With accessory female copulatory organs. FAMILY 4. MESOSTOMIDAE, Dugès. Germarium usually distinct from the vitellarium, pharynx rosulate. *a.* Monogonoporous. *Promesostoma*, v. Gr, M.[1]; *Proxenetes*, Jensen (Fig. III. 3), M.; *Mesostoma*, Dug. (Fig. III. 6), F.; *M. Ehrenbergii* is the subject of a monographic account by Leuckart (44); *Castrada*, O. Schm., F.; *Otomesostoma*, v. Gr., F. *β.* Digonoporous. *Byrsophlebs*, Jensen, male pore anterior to female; germarium single, M. FAMILY 5. PROBOSCIDAE, Carus. The anterior end of the body is modified to form a retractile, tactile organ or proboscis. Germaria usually paired, and vitellaria distinct; pharynx rosulate; very complicated penis; usually monogonoporous. *Pseudo-*

[1] The letter "M" indicates that the genus is Marine and "F" Fluviatile.

rhynchus, v. Gr., M.; *Acrorhynchus*, v. Gr.; *Macrorhynchus*, v. Gr., M.; *Gyrator*, Ehrb. (= *Prostomum*, Oerst.), two genital pores, the female being anterior to the male; *G. linearis*, Oerst., F.; *Hyporhynchus*, v. Gr., M.; *Schizorhynchus*, Hallez (30). FAMILY 6. VORTICIDAE, v. Gr., monogonoporous; mouth usually near the anterior end; accessory female copulatory organ present; pharynx barrel-shaped. SUB-FAMILY 1. EUVORTICINAE, v. Gr., with brain and pharynx well developed; germarium small; free living. *Schultzia*, v. Gr.; *Provortex*, v. Gr.; *Vortex*, Ehrb.; *V. viridis*, with chlorophyll, F.; *Opistoma*, O. Schm. (see 59); *Jensenia*, v. Gr.; *Derostoma*, Oerst., vitellarium reticulate. SUB-FAMILY 2. PARASITICA, v. Gr., pharynx and brain feebly developed; germarium large. *Graffilla*, v. Jher. (see 4), Fig. III. 1; and *Anoplodium*, Schneider; occur parasitic in Gastropoda, and the latter genus in Holothurians; *Syndesmis*, Silliman, parasitic in Echinids, is stated to contain haemoglobin in its parenchyma; *Fecampia*, Giard (20), parasitic in decapod Crustacea, which it leaves when mature. FAMILY 7. SOLENOPHARYNGIDAE, v. Gr. Monogonoporous; single germarium; mouth posterior; pharynx long and tubular; *Solenopharynx*, v Gr.

SUB-ORDER 2. ALLOIOCOELA, v. Gr. Rhabdocoelida, in which the intestine may have irregular caeca; testes numerous (follicular); no conspicuous chitinous copulatory organ. (For an account of this sub-order see 5 and 59)

FAMILY 1. PLAGIOSTOMIDAE. Without an otolith; usually a single genital pore; pharynx variabilis. SUB-FAMILY 1 PLAGIOSTOMINAE, v. Gr. Mouth anterior; pharynx directed forwards; genital pore posterior; germaria and vitellaria *Plagiostoma*, O Schm.; *Vorticeros*, O. Schm. (Fig. III. 7). SUB-FAMILY 2. ALLOSTOMINAE, Bohm. Pharynx directed backwards; mouth posterior *Allostoma*, P. J van Ben (Fig. III. 9); *Enterostoma*, Clap. SUB-FAMILY 3. CYLINDROSTOMINAE, v. Gr A ciliated circular groove; a common enteric and genital pore; a germ-vitellarium. *Cylindrostoma*, Oerst (Fig. III. 8); *Monoophorum*, Bohmig SUB-FAMILY 4 ACMOSTOMINAE, v. Gr. Genital pore posterior. *Acmostoma;* commensal in *Cyprina islandica*. FAMILY 2. MONOTIDAE. With a single otolith; pharynx plicatus directed backwards; paired germaria and vitellaria; digonoporous, M. *Monotus*, Dies.; *M hirudo* is parasitic, *Automolos*, v. Gr FAMILY 3. BOTHRIOPLANIDAE, Vejd. Mouth post-central; monogonoporous; pair of ciliated pits, F. *Bothrioplana*, Vejd. (59).

SUB-ORDER 3. ACOELA, Uljanin. Rhabdocoelida, in which the cavity of the enteron is obliterated by the concrescence of its walls; the mouth leads through a simple pharynx directly into the digestive syncytium; otocyst present; a pair of ovaries (see 6, 24, and 50).

FAMILY 1. PROPORIDAE. Monogonoporous *Proporus*, v. Gr. (= *Schizoprora*, Schm.); *Haplodiscus*, Weldon (62, for recent account see 52); *Monoporus*, v. Gr. (= *Proporus*, Schm) FAMILY 2. APHANOSTOMIDAE, with female pore separate from and in front of male pore, with spermatheca. *Aphanostoma*, Oerst.; *Convoluta*, Oerst.; *Amphichoerus*, v. Gr.; *Polychoerus*, Mark.

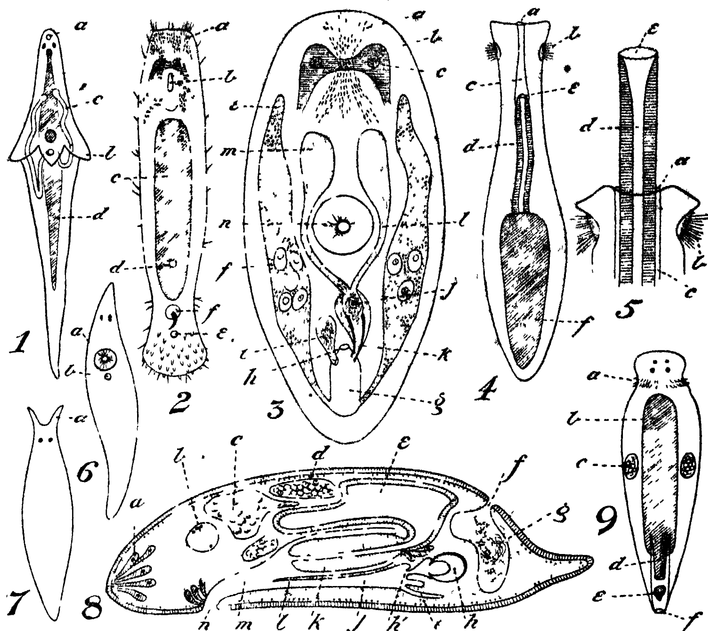


FIG III.—Rhabdocoelida

1 —*Graffilla muricola*, v Jher , parasitic in certain marine molluscs, ventral view *a*, mouth , *b*, three of the four lobes around the body—the ventral lobe overlaps the genital pore (unlettered), the penis, which opens through the same pore as the female ducts, is indicated by the shaded circle , *c*, the left uterus , *d*, the intestine

2 —*Macrostoma hystrix*, Oerst (modified after v Graff), as an example of a "digonoporous" Rhabdocoel Sensory hairs are scattered over the body , and the peculiar fish-like tail carries a number of adhesive papillae *a*, streaks of rhabdite cells , *b*, mouth, leading into the pharynx, immediately in front of which is the brain, on which lies a pair of eye-spots , *c*, the intestine , *d*, the female genital pore , *e*, the male pore , *f*, the penis, which consists of a glandular mass and a curved chitinous spine (black in the figure).

3 —*Proxenetes rosaceus*, v Gr (modified from v Graff), as an example of the "monogonoporous" condition *a*, streaks of rhabdite cells; *b*, brain , *c*, eye , *e*, ovary, which is here a "germ-vitellarium," in which the upper part of the organ gives rise to yolk cells, and the lower part to egg cells, *f*, *g*, the genital atrium , *h*, genital pore , *i*, bursa seminalis or spermatheca, here an evagination of the atrium, but functionally is part of the female system , *j*, seminal vesicle, containing spermatozoa , it is a dilatation of the conjoined sperm ducts , *k*, chitinous tube around the penis , the glandular part of which is indicated by the dotted area , *l*, sperm duct , *m*, testis , *n*, mouth, leading into the rosulate pharynx

4 —*Prorhynchus fontinalis*, Vejd (after Vejdovsky) *a*, terminal mouth ; *b*, lateral, ciliated pit ; *c*, the pharyngeal sac , *d*, the long tubular pharynx in a condition of rest , *e*, its aperture the functional mouth , *f*, intestine

5 —The anterior end of the same Turbellarian, showing the pharynx in the course of eversion (letters as before). The pharyngeal introvert is acrecbolic

6 —*Mesostoma lingua*, O. Schm (after v Gr.), external view *a*, mouth, leading into the pharynx , *b*, the common genital pore. The two black dots in front of the mouth are the eyes

7 —Outline of *Vorticeros* (after v Gr) *a*, tentacular prolongations of the body

8 —*Cylindrostoma quadrioculatum*, Jens A median-longitudinal section (after Bohmig) exhibiting a common oro-genital pore , and the independent, dorsally situated spermatheca. *a*, cephalic glands , *b*, brain ; *c*, testis ; *d*, yolk-producing region of the germ-vitellarium ; *e*, intestine , *f*, pore of spermatheca , *g*, spermatheca filled with spermatozoa ; *h*, penis ; *h'*, its opening into the atrium , *i*, opening of the female duct into the atrium ; *j*, genital atrium , *k*, tubular pharynx, lying in its pharyngeal sac, dorsal to the genital atrium ; *m*, common pharyngo-genital chamber , *n*, oro-genital pore Specialised epidermal unicellular glands are shown opening near this pore, and others into the base of the pharynx.

9 —*Allostoma* *a*, ciliated band behind the head (cf the ciliated pits of *Prorhynchus*), which carries four eyes ; *b*, the intestine , *c*, germarium ; *d*, pharynx, in its pharyngeal sac ; *e*, penis, which opens into a genital atrium, communicating with a common "pharyngo-genital chamber", *f*, the "oro-genital pore."

Further Remarks on the Rhabdocoelida.—The Rhabdocoelid Turbellaria contain forms which approach more nearly than do any other of the orders to the ancestral Platyhelminth. The anteriorly placed mouth, the comparatively simple "sucking pharynx," leading into a simple, straight intestine; the symmetrical condition of the excretory organs; the "compact gonads," and the frequent occurrence of "ovaries"—without differentiation into germ-producing and yolk-producing regions—all agree with a generalised flatworm. Nevertheless, the nervous system in the Rhabdocoela is much more highly differentiated than in the Polycladida. Of the three sub-orders included in the Rhabdocoelida it is amongst the Rhabdocoela that we find these simple conditions, *e.g.* amongst the Macrostomidae; for the Acoela, which von Graff places at the base of the Turbellarian tree, present every evidence, anatomically as well as embryologically, of degeneration. The Alloiocoela, through *Bothrioplana*, lead onwards to the Tricladida. Whilst the Polycladida are descended from the Rhabdocoela along another line.

The Rhabdocoela are represented abundantly in fresh water, and in the sea; some few genera even are ectoparasitic; the Acoela are marine, as also are the Alloiocoela, with the exception of *Plagiostoma lemani* in the deep water of Swiss lakes (Duplessis), and *Bothrioplana*, which occurs in springs. In form they are flat or cylindrical, but with flat ventral surface; ovoid, with frequently the posterior end pointed.

The epidermis in Rhabdocoelida as in the rest of the Turbellaria consists of a single layer of ciliated cells (discovered by Fabricius), which are usually columnar or cubical in shape (Fig IV.) Belonging to this layer, though in Rhabdocoelida usually sinking below it, are gland cells of two chief kinds · (*a*) cells producing unformed secretion or "mucus"; these are specially developed, though not exclusively, on the ventral surface; and (*b*) cells producing "formed secretion"; the products of these cells are either—

(A) Finely granular, block-like masses, with uneven surface, pseudorhabdites, v. Gr. (schleimstabchen, Lang), (IV. 2, *c*), especially in the Alloiocoela; (B) spindle-shaped, homogeneous, refringent rods, with smooth surface, "rhabdites" (discovered in Rhabdocoeles by O. Schmidt; and in Polyclads by Quatrefages), (IV. 7); (C) or each cell may produce a capsule or cyst (sagittocyst), (IV. 8, 9), in which is contained a single spindle-shaped needle (these are rare in Rhabdocoela); or finally (D), in rare instances nematocysts (Leuckart, 1848), (IV. 10), (*Microstoma* and *Stenostoma*). The occurrence of nematocysts, quite similar to those of *Hydra*, in several Turbellaria, and in certain Nudibranch Molluscs seems to indicate the very close relationship of these two groups with the Coelenterata.

It is by no means certain that the "rod cells" of the Turbellaria are the direct descendants of cnidoblasts of the ordinary Coelenterate; more likely is it that they have a close affinity with the

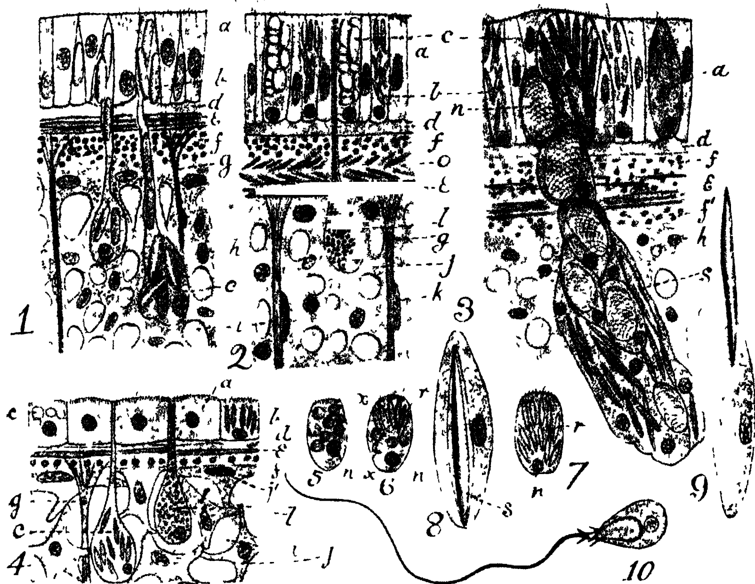


FIG. IV—The Microscopic Structure of the Body Wall in Turbellaria

1—A Triclad (after Woodworth) *a*, epidermal cell, *b*, rhabdites or rods, formed in sub-epidermal cells, and passing upwards between the ciliated cells, *c*, a sub-epidermal bacilliparous or rod cell In many Triclads these cells do not sink below the epidermis, *d*, basement membrane, *e*, circular muscles, *f*, longitudinal muscles, *g*, vertical muscles, *h*, nucleus of parenchymal syncytium, *i*, lacunae in the parenchyma

2—A Polyclad (combined from Lang's figures) *a*, epidermis, *b*, rhabdite cell, *c*, "pseudo-rhabdites" in an epidermal cell, *j*, parenchymal syncytium, *k*, the nucleus of a muscle cell (or myoblast), *l*, gland cell, *o*, oblique or diagonal muscles, *d*, *e*, *f*, *q*, *i*, as before

3—The Polyclad *Anonymus* (after Lang) *a*, *b*, rhabdite cells, another in the middle is in the act of discharging a rhabdite, *c*, "needles" (striated rods) in their parent cell, *n*, nematocyst in its parent cell, this is the uppermost of a tract of cells containing other nematocysts, needle cells, and a sagittocyst, such a tract constituting a *waffenstrasse* is rare amongst Polyclads, but common enough amongst Rhabdocoels, where it is formed, however, usually, of rhabdites only, *S*, a sagittocyst, *f*, outer, and *f′*, inner layers of longitudinal muscles, other letters as before

4—A Rhabdocoel (combined from Vejdovsky, etc.) *b*, rhabdite cell, in its primitive position, as occurs in some forms, *c*, sub-epidermal rhabdite cell, such as occurs in other forms; *c′*, an epidermal cell, in which rhabdites are commencing to be formed, *j*, branched, central parenchymal cell, *j′*, peripheral parenchymal cells, *i*, intercellular lacunae, other letters as before

5, 6, 7—Three stages in the development of rhabdites in epidermal cells of the Polyclad *Thysanozoon* (from Lang) *n*, nucleus of cell, *x*, refringent globules of secretion which develop into the rhabdites (*r*)

8.—A sagittocyst from the acoelous genus *Convoluta* (from v. Gr). *s*, the sagitta.

9—The same, discharging its sagitta.

10.—A nematocyst from the Rhabdocoelid *Microstoma lineare* (after v. Gr.). The thread is everted, but the cyst itself remains embedded in its parent cell or "cnidoblast."

adhesive cells of Ctenophora. But the existence of true nematocysts in several species does not forbid us deriving the group from a more generalised Coelenterate.

It appears that when discharged, the first two structures swell up, or contribute to form the slimy material with which the animal invests itself on irritation. It is still uncertain what is the chief function of the rhabdites; whereas Max Schultze regarded them as serving to increase the sensitiveness of the skin, others believe they give a firmness to the body. It should be mentioned that a considerable number of Rhabdocoela have no rhabdites; and that these are frequently commensal or parasitic, viz. species of *Proxenetes*, *Graffilla*, *Fecampia*, *Acmostoma;* and amongst non-parasitic forms, *Cylindrostoma*, *Plagiostoma*, *Prorhynchus*.

Below the epidermis is a distinct basement membrane, into which the muscles are attached (IV. *d* in all figs.). In the Rhabdocoelida the musculature consists of an outer layer of circular fibres and a deeper layer of longitudinal ones, between which in larger forms is a layer of diagonal fibres. In addition, dorso-ventral muscle cells traverse the parenchyma in a more or less definite way; they are only feebly developed in the Acoela. The muscle cells are all smooth, and those running dorso-ventrally are branched at each end.

The characteristic connective tissue of the Platyhelmia occupying the space between the dermal muscles and the viscera is termed "parenchyma" (or mesenchyma, Bohmig). This mesoblastic tissue gradually fills the blastocoele of the embryo. In the adult Rhabdocoelida it appears to consist of branched cells, which may be vacuolated, and so give rise to intracellular spaces (Fig. IV. 4); the processes of the cells unite with their neighbours and enclose intercellular spaces or lacunae, which may communicate with one another and so form a sort of rudimentary lymphatic or vascular system, this seems to be a fairer comparison than to regard these spaces as coelomic; the true nature of this tissue is, however, by no means agreed upon by the various authorities; and, indeed, it appears to differ in the different orders of Turbellaria. In this connection reference may be made to the peculiar connective tissue of the Mollusca, in the interpretation of which precisely similar antagonistic views have been held by various authorities In the lacunae is a fluid which is frequently coloured; and in *Syndesmis* (Cuenot) and *Derostoma* it is said to contain haemoglobin. The parenchymal cells themselves are frequently loaded with pigment granules, giving colour to the animal. In some Alloiocoela this parenchyma is almost entirely confined to the marginal region of the body, and may even form a definite layer immediately within the longitudinal muscles (59). In many of the Acoela this peripheral parenchyma differs from that occupying the greater part of the body (central parenchyma) which is of much looser character, but it again gradually becomes more compact as the axis of the body is approached (see Bohmig, 6); and in

such forms as *Convoluta* and *Haplodiscus* there is occupying the central region a compact mass of nucleated protoplasm, in which cell outlines are not distinguishable (Fig. V. 7, 8). In this axial syncytium the remnants of prey are found; it is the "digesting parenchyma," or more properly, the syncytial hypoblast; in *Proporus* and others this digesting parenchyma is represented by separate amoeboid cells, which extend throughout the central parenchyma; in this latter case, the hypoblast cells which in the embryo surround a true enteron, have wandered in all directions; in the former case, the cells have fused to form a more concentrated syncytium.

In *Convoluta Schultzii*, *Vortex viridis*, and a few other species, chlorophyll bodies or (in *C. paradoxa*) yellow cells occur in the peripheral parenchyma; it has been shown experimentally that these bodies behave like the chlorophyll bodies of green plants, and they appear to be of considerable importance to the animal, which then presents the "holophytic" mode of nutrition. How far these bodies, which are similar to those occurring in Anthozoa, to which Brandt has given the name Zoochlorella, are part and parcel of the animal, or whether they are symbiotic algae is still a matter of dispute. Haberlandt (28) finds that they are nucleated, but without a cell wall (Fig. V. 3, 4, 5); that when isolated they cannot form a cell wall, and soon die, and in fact are unable to lead an independent existence. They appear to be algae, or flagellata (similar to *Chlamydomonas*), but so adapted are they to a symbiotic existence, that they now form a definite and inseparable part of the tissues of the worm and function as assimilating organs, at the same time providing, by their disintegration, food for the Planarian (Geddes, 19)

The nervous system in the primitive Turbellarian was no doubt similar to that which occurs in the Polycladida, viz. a network of nerve fibres and cells which had already sunk below the dermal muscles, arising from or converging to a definite group of ganglion cells forming a "brain" near the anterior end of the body. The nervous system as presented by the majority of Rhabdocoela has lost its ancestral character of a network; there is a pair of well-developed cerebral ganglia near the anterior end of the body, whence four pairs of nerves arise, of which one pair lying along the ventral surface is especially stout: other nerves go forwards. In the Alloiocoela a few transverse commissures may occur between these nerves; whilst in Acoela, in which a network occurs (Fig. V. 1), the nervous system, apart from the brain, presents a comparatively primitive condition. There may also be a nerve plexus in the wall of the pharynx. The brain was first correctly interpreted as such by Ehrenberg, 1836. It had previously been regarded as the "heart," while Dugès held the nerves for "blood-vessels."

As sense organs, the Turbellaria present eyes which are simple, epidermic, pigment spots in Acoela, and in a few other cases, but they usually sink below the epidermis and lie in the parenchyma;

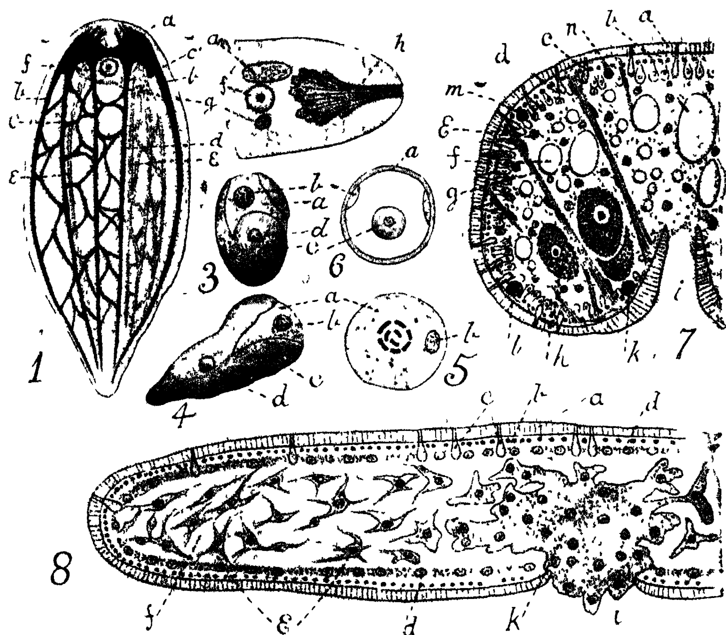


Fig. V.—Anatomy of the Acoela

1.—The nervous system (modified after Bohmig) *a*, brain, *b*, marginal (lateral) nerve, *c*, dorso-lateral nerve, *d*, dorsal nerve, *e*, ventral nerve. The nervous network of the dorsal surface is represented on the left, that of the ventral surface on the right, where the dorso-lateral nerve (*c*′) is cut short. *f*, otocyst, *g*, ventral nerve commissure connecting the two ganglionic masses (*a*) of the brain.

2.—Longitudinal section through the anterior end of the body. *a*, brain, *g*, ventral commissure; *f*, otocyst, *h*, frontal gland.

3 and 4.—Chlorophyll bodies of *Convoluta* (after Haberlandt). *a*, protoplasm of the cell, *b*, its nucleus, *c*, chloroplast or envelope of chlorophyll, *d*, pyrenoid.

5.—Section through a chlorophyll body (after Haberlandt). The black dots in the centre of the cell are starch granules, *b*, the nucleus.

6.—Otocyst. *a*, the wall formed of two cells, *b*, one of the two nuclei, *c*, the otolith cell with its nucleus.

7.—Half a transverse section across *Convoluta* in the region of the mouth (after v. Graff). *a*, epidermis; *b*, muscular coat, consisting of outer circular, and inner longitudinal fibres, *c*, gland cells opening on to the surface; *d*, peripheral parenchymal cells, *e*, nucleus of deeper parenchyma cells, *f*, lacunae in the parenchyma, *g*, dorso-ventral muscles with their nuclei, *h*, ovum, in the ovary, which is not marked off in any way from the surrounding parenchyma, *i*, mouth opening directly into the central mass of parenchyma, *k*, ventral nerve tract, *l*, marginal nerve, *m*, dorso-lateral nerve; *n*, dorsal nerve. The chlorophyll bodies are omitted.

8.—Half of a transverse section of *Haplodiscus* (after Bohmig), to show the differentiation of the parenchymal tissue into (*d*) peripheral syncytium, with round nuclei forming a layer underlying the muscular coat, *e*, intermediate or general mass of amoeboid and star-shaped cells, and *k*, a digesting, central syncytium, other letters as in 7.

they then have a definite and peculiar structure. An otocyst, discovered in *Monocelis* by Frey and Leuckart, occurs in the Acoela (Fig. V. 6), the Monotidae, and *Mecynostoma*. Ciliated pits

(originally observed by O. Schmidt), sense organs of peculiar character similar to those which exist in many *Annelida*, also occur in Microstomidae, Plagiostomidae, and a few others (III. 4; VII. 5); the pit rests upon a group of ganglion cells, which is directly or indirectly connected with the brain; these may, perhaps, be the precursors of the elaborate "cerebral organs" of the Nemertines.

Another character of the Nemertines, the "proboscis" (as Leuckart first pointed out), is foreshadowed in the family *Proboscidae* (VI. 1-7). In all Turbellaria the anterior end of the body is specially provided with tactile hairs; and in several genera this region is capable of a slight invagination. In this family the simplest stage is represented by *Pseudorhynchus*, in which the anterior end of the body is deprived of cilia, somewhat prolonged and capable of freer movement than usual by the action of numerous short muscles. In the remainder of the family this "snout" is permanently withdrawn into a pouch, which usually lies at the tip of the body, but may be subterminal and ventral (*Hyporhynchus*, Fig. VI. 5); the snout or proboscis now consists of a mass of muscles, and is capable of protrusion, while withdrawal is performed by four long retractor muscles. The "frontal organ" of Acoela was at one time thought to be a similar sense organ; but v. Graff (24) has shown that it is entirely glandular (Fig. V. 2), containing neither muscle nor sense cells.

The sub-order Rhabdocoela possess an intestine which retains much of the ancestral character; it is a straight and simple elongated sac (Fig. III. 2, 4). The intestine may be constricted by the ripe gonads, and by the development of dorso-ventral muscles to form incomplete "septa"; this leads to a lobing such as occurs in Alloiocoela (Fig. VIII.), which reaches its highest phase in *Bothrioplana*, where the lobes become long and regularly placed; the large pharynx of this genus, placed posteriorly, indents, as it were, the gut, which now passes on each side of it, and has quite the appearance of that of a Triclad.

The mouth retains its primitive position near the anterior end in a considerable number of forms, though it may occupy any position on the ventral surface, this mouth leads directly into the digestive parenchyma (hypoblastic syncytium) in Acoela, though frequently the epidermis is slightly invaginated, and the muscular coats are here thicker (Fig. V. 7, 8). This is ontogenetically what happens in the other groups in which a distinct pharynx is formed. This pharynx has various shapes within the group of Turbellaria, which have received various names (Fig. VI. 8-13); the two chief varieties distinguished are: (*a*) *Ph. bulbosus*, in which the muscles of the pharyngeal wall are surrounded by a distinct sheath, separating them off from the parenchyma. This type of pharynx, which is used for sucking and cannot be protruded far, occurs in the

majority of the Rhabdocoelida under some form or another. (*b*) *Ph. plicatus*, in which the sheath is absent, is characteristically developed in the other two orders; it is really an acrecbolic introvert and occurs under two forms, which perhaps represent two stages in development. In the Polycladida the pharyngeal sac is of considerable diameter, with its axis at right angles to that of the intestine; the pharynx has the form of a freely projecting muscular fold arising from the circumference of the sac, than which it is frequently larger, and is, therefore, much folded when

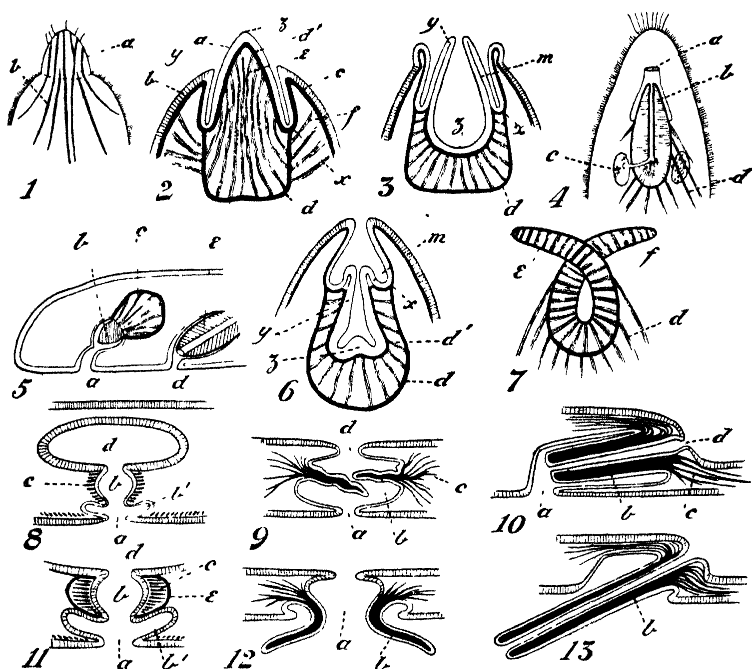


Fig. VI.

at rest; when brought into use this muscular organ is protruded through the mouth, and is then spread out so as to envelop the prey (Fig. VI. 9, 12). In a few of the Polyclads the axis of the pharyngeal sac shifts so as to lie nearly parallel to that of the intestine instead of at right angles to it; and the entrance to the intestine is no longer directly over the oral aperture; the muscular fold now loses its irregular shape, and its base becoming smaller it forms a muscular cylindrical tube; this is the form of pharynx characteristic of the Tricladida (Fig. VI. 10, 13). Glands, more or less abundant, exist in or around the pharynx, pouring their

secretion into its lumen. As to the structure of the intestine, it is chiefly interesting from the fact that some of the epithelial cells can thrust out pseudopodia and directly take in food particles. We have thus a starting-point for that syncytial condition of the hypoblast which occurs in the Acoela.

The excretory system or "water-vascular system" was first identified by Ehrenberg; while O. Schmidt added greatly to our

FIG. VI.—Figs. 1 to 7 illustrate the Structure of the "Proboscis" of the Proboscidae.

1.—The anterior end of *Pseudorhynchus bifidus*, v. Gr. *a*, the introversible non-ciliated tip of the body; *b*, the isolated strands of longitudinal muscles which act as retractors of this proboscis.

2, 3, and 6 refer to *Macrorhynchus* (after v. Graff). *a*, the non-ciliated epidermis of the proboscis; *b*, the ciliated epidermis of the body, represented in all three diagrams by the vertically shaded region; *c*, the muscular coat of the body wall, which at *x* splits into two sheets, forming (*d'*) a sub-epidermal or outer sheath of the proboscis, and (*d*) the inner sheath. The former (*d'*) can be withdrawn from the epidermis which appears to slide over it, as in 3 and 6. Between these two sheaths and inserted into them at each end are the intrinsic muscles (*e*) of the proboscis; *f*, the retractor muscles (which are omitted in Figs. 3 and 6). The points marked *x*, *y*, *z* deserve attention. In 2, *z* marks the apex of the everted proboscis; *x*, the point at which the muscular sheaths (*dd'*) separate; *y* a point about half-way along the side of the proboscis. In 3, the apex *z* and the upper half of the proboscis have been entirely withdrawn by the active contraction of the intrinsic muscles of the proboscis, so that the point *y* now marks the lip of a cup. The outer sheath has been pulled away from the epidermis between *x* and *y*. In 6, the proboscis is entirely retracted, the side as marked by the point *y* having followed the apex, and lies half-way down the cup. This further process is partly due to the retractor muscles. As the inrolling of the sides takes place, the outer sheath (*d'*) resumes its normal position against the epidermis, and the gap *m* is reduced.

4 and 7.—The proboscis of *Schizorhynchus* (after Hallez). 4. The anterior end of the worm, the proboscis being at rest; *a*, the aperture of the proboscis sac on the ventral surface of the body; *b*, the proboscis consisting of two halves, leaving a channel between them, into which open the ducts of glands (*c*), the duct on the right side is supposed to be cut away; these glands are probably poisonous and represent the scattered, diffuse glands on the proboscis of *Macrorhynchus* and others; *d*, retractor muscles. 7. The proboscis of *Schizorhynchus* everted (the surrounding parts are omitted). *e*, the muscular sheath; *f*, intrinsic muscles.

5.—Side view of the anterior end of *Hyporhynchus* (after v. Graff). *a*, the entrance to the proboscis sac; *b*, glandular part of proboscis; *c*, intrinsic muscles surrounded by the sheath; *d*, mouth; *e*, pharynx.

8-13 illustrate the chief varieties of pharynx in the *Turbellaria*. *a*, mouth; *b*, pharynx; *b'*, prepharynx, or pharyngeal sac; *c*, intrinsic muscles; *d*, entrance to intestine. 8. Diagrammatic section across the middle of a Rhabdocoel. *a*, mouth leading into a "pharynx simplex" whose muscles (*c*) are not separated from the parenchyma; *d*, the intestine, the dorsal wall of which, as well as dorsal body wall, is represented in this, but is omitted from the subsequent diagrams.

11.—A "pharynx bulbosus," in which the muscles of the pharynx are cut off from the parenchyma by the sheath (*e*); the pharyngeal sac is better developed. This type of pharynx is very frequent in Rhabdocoela, and is universal amongst the Trematoda.

9 and 12.—The "pharynx plicatus" typically developed in the Polyclads consists essentially of a circular, horizontal fold (*b*) of the muscular wall of the pharyngeal sac. The muscles spread outwards to be inserted in the body wall and act as retractors of the fold. On eversion (12) the folded membrane spreads outwards and envelops more or less of the prey; the pharynx is thus turned inside out.

10 and 13.—The tubular pharynx, typically developed in Triclads, but occurring elsewhere. 10 at rest, 13 protruded. It is essentially an acroecbolic introvert, which can elongate and contract by the action of its intrinsic muscles, and is withdrawn into the pharyngeal sac by the retractors; in these diagrams there is no attempt to represent the complex arrangement of muscular fibres in the substance of the pharynx itself.

knowledge of the general plan of the system. Typically, there are in the Rhabdocoela two main canals, each with a pore posteriorly (Fig. VII. 1), or they may unite to form a short common duct before opening by a median pore; and the fusion may go so far as to give rise to a single median canal (*Stenostoma*). In *Mesostoma* each lateral canal opens into the peripharyngeal sac by means of a transverse canal, or (Prorhynchidae) the two canals open anteriorly by a median pore. The course of this set of tubules has recently

been carefully worked out by Vejdovsky for *Bothrioplana* (Fig. VII. 5); the flame cells are in two series, one dorsal and another ventral. In the Acoela it is doubtful whether an excretory system

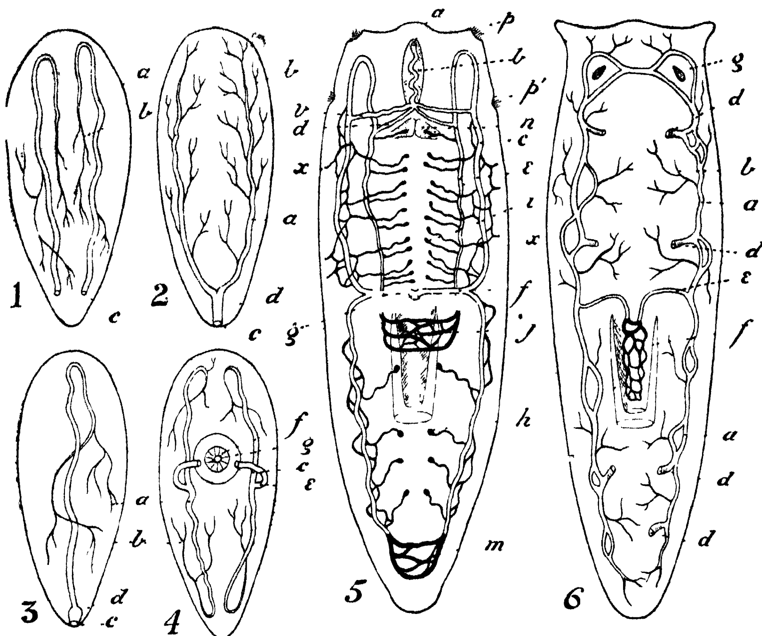


FIG VII.—The Chief Plans of Arrangement of the Main Canals of the Excretory System in Rhabdocoels (Figs 1-4), after v Graff, Alloiocoel (Fig 5), after Vejdovsky, and Triclad (Fig 6), after Ijima

1.—*Derostoma* presents the most primitive arrangement, each of the paired excretory pores (c) leads into a main canal or duct (a), whence capillaries (b) are given off, terminating in flame cells By the approximation of the ducts posteriorly, and subsequent fusion of their hinder ends, the condition represented in 2, for *Plagiostoma* arises where the median posterior pore leads into a short common duct A further step results in the total fusion of the two ducts along their whole extent, as in 3, *Stenostoma*, and a specialisation of the terminal part of the common duct gives rise to a contractile bladder (d)

4.—*Mesostoma* Here the two excretory pores have become involved in the invagination which forms the pharyngeal sac (g), in which lies the pharynx (f)

5.—In *Bothrioplana* there are two median excretory pores, one anterior (a), and one near the centre of the body (g), both on the ventral surface The latter appears to have been derived from the condition seen in *Mesostoma*, by the approximation and fusion of the transverse excretory ducts The main canals on either side have the normal condition, being recurved at the anterior end, and the four canals so formed appear to have effected a secondary communication with the exterior a, anterior pore leading into a duct (b) with contractile wall, dorsal canal (d) entering the dorsal or recurrent limb (e) of the main lateral canal, ventral branch (v) enters the main canal (c), which is connected with a plexus of capillaries along its whole extent, the right and left canals being connected at the posterior end of the body by the plexus m The lateral plexus gives off at intervals short branches (xx) which pass towards the surface of the body; but no pore has been detected From this lateral network there arise mesially a definite number of branches, each terminating in a flame cell (h), of which five lie in front of, and four behind the pore (g) A second series of flame cells (i), seven in number, are carried by branches from the dorsal stem, the latter terminates in a plexus (j) above the pharynx n, the brain, p, p′, the two pairs of ciliated pits (The two median plexuses are represented too strongly.)

6.—Plan of a Triclad. a, main canal opening at d, d to the exterior, there are four or five pores not strictly symmetrical in arrangement. Each main canal gives rise to a branch (e) which gives origin to a plexus (f) in the substance of the pharynx (according to Chichkoff). g is the eye.

exists. Geddes (19) described certain structures under the name "pulsatellae," which Yves Delage (12) regards as isolated flame cells; but these have not been described by more recent observers.

The generative organs of the Turbellaria, as in all Platyhelmia, are very complicated; but they present more variations in detail in the Rhabdocoelida than in the other orders, and a given plan does not hold even within the same family. The male organs consist of a pair [1] of testes, from each of which a sperm duct passes backwards to open into a seminal vesicle, whence a duct perforates a glandular and muscular organ or penis, which is frequently armed with chitinous spines or a chitinous sheath, the character of which is of generic and specific value. The penis opens into an epiblastic sac known as the "atrium genitale," if it is common to the male and female organs, or the duct of each sex may have its own "antrum" and external pore. We have either a monogonoporous (Fig. III. 3) or a digonoporous condition in the Rhabdocoelida, and the female pore may lie in front of the male pore (Fig. III. 2). The genital pore was first recognised as such by Johnson (36) in *Planaria torva*, previously it had been regarded as the anus. The penis appears to be used as much in catching prey as in copulation, and in *Macrorhynchus helgolandicus*, in which a poison gland traverses the organ, it appears to be entirely used for this purpose; and no doubt the arrangement in *Prorhynchus*, where the penis opens at the same pore as the pharynx, and is armed with a perforated spine, has come about by the employment of this organ in catching prey (32 and 39).

In the sub-order Rhabdocoela the testis of each side retains the ancestral condition of a "compact," tubular organ (Fig. VIII.); but in the Alloiocoela and Acoela this single testis becomes constricted (? by dorso-ventral muscles) into a number of "follicles," which lie near the anterior end of the animal, each follicle of which ontogenetically is derived from a single cell. Despite the most careful recent research, the sperm duct has not been traced up to each one of these follicles, and it is uncertain how the spermatozoa pass from them to the seminal vesicle. One of two methods has been suggested: (*a*) that by the enlargement of the follicles they come to open into one another, and so communicate ultimately with the sperm duct, or (*b*) they burst into the parenchymal lacunae, and their contents thus gain the duct. In some cases (*Acoela*) the duct is not even continuous with the seminal vesicle.

With regard to the female organs, there can be little doubt but that in the primitive gonad egg cells were formed and supplied with yolk by their neighbours; such an organ or "ovary" occurs in Acoela (Fig. VIII.) and in many Rhabdocoela as a single or

[1] Haswell (32) states that in *Prorhynchus* sp. the male organs are only on the right side, and the female only on the left side, unpaired in each case.

paired structure. Later, one part of this gland came to give rise to germ cells, whilst the rest of it gives rise to cells similar in origin, but loaded with yolk spherules. When the egg cells are laid they are surrounded by these yolk or vitelline cells, upon which the young embryo will feed; such a gland, forming the two kinds of cells in different parts, is sometimes called a "germ-vitellarium" (Fig. III. 3). We find one or a pair of such organs

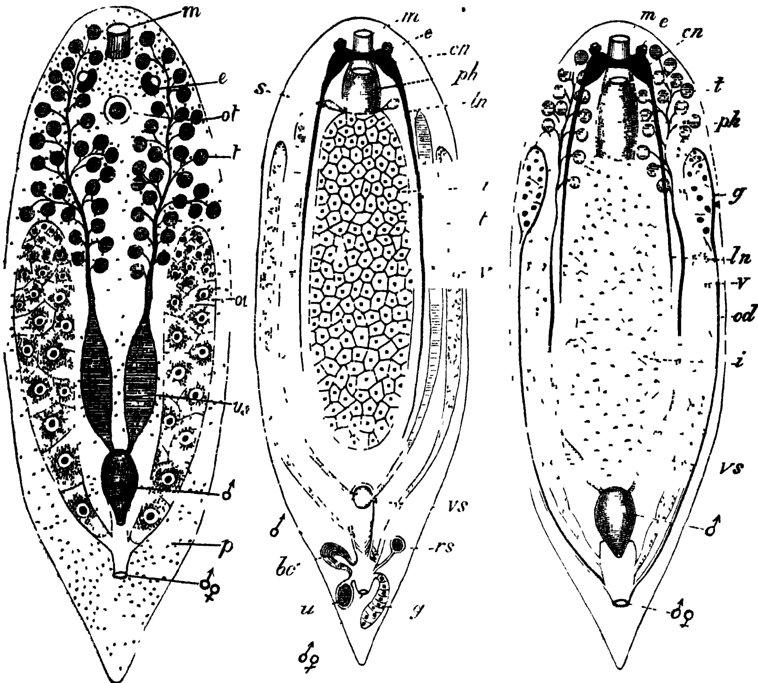


FIG VIII

Plans of structure of Rhabdocoelids (from v Graff) Left-hand figure is an Acoelous, the middle is a Rhabdocoelous, and the right-hand is an Alloiocoelous Turbellarian *bc*, bursa copulatrix, *cn*, cerebral ganglion, *e*, eye, *g*, germarium, *i*, enteron, *ln*, ventral nerve cord, *m*, mouth, *ot*, otocyst, *ov*, ovary, *p*, digesting parenchyma, *ph*, pharynx, *rs*, spermatheca, *s*, salivary gland, *t*, testis; *u*, uterus, containing an egg, *v*, vitellarium, *vs*, seminal vesicle, ♂, chitinous penis, ♂ ♀, genital pore.

amongst the Rhabdocoelida. Further, this differentiation of function may become so complete that the yolk-forming part becomes entirely separated from the germ-forming region, so that a "vitellarium" becomes distinguishable from a "germarium" (Fig. VIII.); each organ has its own duct, which may or may not join before entering the female antrum. This differentiation of the "ovary" into two parts was first understood by O. Schmidt. Amongst the Rhabdocoelida we have instances of a pair of germaria

(more rarely a single one) and a pair of vitellaria, usually compact, but the latter may branch and anastomose to form an apparently single reticulated organ, but the two ducts indicate its double nature. The accessory female organs are no less varied (Fig. VIII.). A spermatheca, either as a swelling on the common duct, or finally as an outgrowth of the atrium, may be present. A bursa copulatrix (or vagina) may exist or not; but there is usually a sac in the Rhabdocoela in which the cocoon is retained; this function is originally performed by the atrium, but in most cases a diverticulum of this chamber, provided with glandular walls, receives the name "uterus."

Reproduction.—Our knowledge of the development of the Rhabdocoelida is very scanty; in most genera each egg cell becomes enclosed together with numerous yolk cells within a hard capsule, which is secreted by special gland cells. Sometimes the egg is only set free by the death of the parent. This capsule, which has characteristic shapes, is attached to water plants. Segmentation results in the formation of micromeres and macromeres; gastrulation is effected by epibole, and when the embryo has attained a stage with a distinct gut and pharynx it devours the surrounding yolk cells.[1] It is important to note that the animal is at first nearly spherical, and the mouth central, but by differentiation in growth the mouth becomes carried forwards or backwards as the case may be.

In some forms (*Mesostoma*) the winter and summer eggs differ; the summer ones, having a thin shell, undergo development in the parent's body, as is the case in the Crustacean *Daphnia.* But perhaps the most interesting fact is that amongst the Microstomidae a mode of asexual reproduction takes place during summer, and the genital organs only mature in the autumn. The fact that Turbellaria can reproduce in this way seems to have been observed first by Dreparnaud (1803); but in 1822 J. R. Johnson made further observation on the matter, and M. Faraday (16) carried out some interesting systematic experiments on this subject, both these authors were greatly in advance of their contemporaries in this matter. This asexual process resembles, in the main, that which occurs amongst the Naids (Oligochaeta) and Syllids (Polychaeta), in that, after attaining a certain size, the animal becomes partly constricted; an active production of cells takes place at the anterior end of this young zooid, by which a new brain and a new pharynx are formed. After this process has gone a certain length, a new constriction and new budding take place near the end of each of the two zooids; in this way is formed a chain of four, eight, or

[1] In the acoelous *Polychoerus* there is no trace of an enteron (see Gardiner, *Journ. Morph.* xi. 1895, p. 155).

sixteen zooids (Fig. IX.), which will ultimately separate from one another and proceed to live an independent life, reproducing in the same way till some change in temperature or food supply intervenes; then the genital organs appear, and sexual reproduction takes place (see 61, 60, and 38) It is generally stated that *Microstoma* differs from other Turbellaria in being unisexual, but such is not the case; it is a protandrous hermaphrodite.

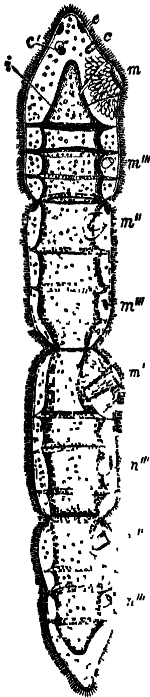


Fig IX.

Order 2. **Tricladida.**

Turbellaria, in which the intestine consists of three main branches: one median anteriorly directed, and a pair of posteriorly directed lobes, each of which gives off a series of caeca. The mouth is post-central; the pharynx tubular; there is a single genital pore common to the two sexes (monogonoporous). For an account of the anatomy see 7, 34, and 41.

There are nine families, which Hallez (31) arranges in three tribes.—

Tribe 1 Maricola Marine Triclads, with intestinal caeca only slightly branched; body depressed; uterus usually behind the genital pore.

Fig IX

Microstoma lineare, Oerst, undergoing division (from v. Graff) The individual has first divided into two, [illegible], and each of these has again divided Each of the four zooids has again divided into two, and so on, till sixteen individuals are here marked out *m*, mouth of original animal, *m'*, mouth of the hinder of the two individuals into which it divided, *m''*, the two mouths of the third generation, *m'''*, the four mouths of the fourth generation [illegible] the eight individuals of the fifth generation have not yet [illegible] *c*, ciliated pits, *e*, eye-spots, *i*, intestine

Family 1. Otoplanidae, with a pair of ciliated pits and a median otocyst. *Otoplana*, du Plessis. Family 2. Procerotidae, with otocyst, but no ciliated pits. *Cercyra*, Schm., *Fovia*, Stimpson; *Gunda*, O. Schm. (see Lang, 41): *Uteriporus*, Bergendal; *Micropharynx*, Jagersk, on *Raia batis*. Family 3. Bdelluridae, with a caudal fixing apparatus, developed in relation to their parasitic habits. There are no rhabdites; two independent uteri or spermathecae, each with an independent pore. *Bdellura*, Leidy; *Syncoelidium*, Wheeler; both occur fixed to gill hooks of *Limulus*, on which they deposit their egg capsules (see 63).

Tribe 2. Paludicola. Fluviatile forms, in which the intestinal caeca are usually much branched; the uterus lies between pharynx and penis.

Family 4 Planariidae. *Planaria*, O. F. M; *Dendrocoelum*, Oerst; *Euplanaria*, Hesse; *Dicotylus*, Grube (27), (Fig. X 5), *Anocelis*, Stimps; *Oligocelis*, Stimps.; *Polycelis*, Hemp and Clap.; *Phagocata*, Leidy (Fig. XI. 2, see 65).

Tribe 3 Terricola. Terrestrial forms, in which the intestinal caeca are merely lobed; mouth variable in position; form of body variable;

uterus rudimentary; ventral body musculature well developed (see 13, 26, 47).

FAMILY 5. LEIMACOPSIDAE. Dorsal surface very convex; mouth pre-central. *Leimacopsis*, Dies. FAMILY 6. GEOPLANIDAE, v. Gr. Land Planarians without tentacles or suckers; eyeless, or with many marginal eyes. *Geoplana*, Stimpson (Fig. X. 3); *Pelmatoplana*, v. Gr.; *Choeradoplana*, v. Gr.; *Polycladus*, Blanch.; *Artioposthia*, v. Gr.; *Geobia*, Dies. FAMILY 7. BIPALIIDAE. Anterior end is broadened out to form a semicircular cephalic plate; marginal eyes. *Bipalium*, Stimpson (Fig. X. 1); *Perocephalus*, v. Gr.; *Placocephalus*, v. Gr.; *P. kewensis*, Moseley. FAMILY 8. COTYLOPLANIDAE, v. Gr., with sucker on ventral surface anteriorly, and with two spherical eyes. *Cotyloplana*, Spencer (57, Fig. X. 4); *Artiocotylus*, v Gr. FAMILY 9. RHYNCHODEMIDAE, v. Gr, with two spherical eyes anteriorly. *Platydemus*, v Gr.; *Dolichoplana*, Mos.; *Rhynchodemus*, Leidy; *Microplana*, Vejd.; *Amblyplana*, v. Gr.; *Nematodemus*, v Gr.; *Othelosoma*, Gray.

Further Remarks upon the Tricladida.—The distribution of these forms on land, sea and fresh water, is of great interest, though it remains to be seen how far Hallez's classification on this basis is justified.

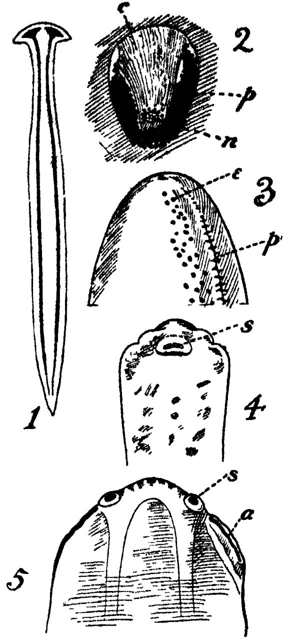


FIG X

1 – *B*[illegible] Moseley, showing the characteristic head of the family, and the longitudinal colour-markings so common in terrestrial Triclads

2 —Unicellular eye of *Geoplana* (after Dendy) *c*, refringent portion of the cell, *n*, nucleus, *p*, peripheral pigment of the cell

3 —Side view of the anterior end of *G Spenceri*, Dendy, showing numerous eye-spots (*e*) and the row of ciliated pits (*p*).

4 —*Cotyloplana whitelegii*, Spencer, ventral view of the anterior end. *s*, the preoral sucker (After Spencer.)

5 —*Dicotylus pulvinar*, Grube, dorsal view of the anterior end, showing (*s*) the sucker on each side, (*a*) the "lateral groove," which is perhaps ciliated (After Grube.)

In general form they are flat and leaf-like, though the terrestrial species are usually elongated, some attaining a length of nine or even fourteen inches Ferussac, 1841, appears to have been the first to describe a land Planarian from Brazil. Since that time they have been found in nearly all parts of the world (by Moseley, Darwin, Dendy, etc.). The Triclads are carnivorous and nocturnal. Their distribution seems to indicate that they are ancient forms; nevertheless, they have in many respects lost their primitive characters, and present a greater degree of complexity and differentiation than do the Rhabdocoelida. The majority are longer and narrower than in other orders; the anterior end is frequently eared (*Planaria*), or with tentacles (*Leimacopsis*),

or extended to form a crescentic or hammer-shaped plate (*Bipalium*), and may even bear suckers (*Dicotylus, Cotyloplana*).

The rod cells sink into the parenchyma, and are connected with the epidermis by "rod tracts" (Fig. IV. 1). Peculiar V-shaped rods have been recorded in *Placocephalus* (Shipley). In a few genera rhabdites are absent (*Bdelluridae*).

The parenchyma appears similar to that in Rhabdocoela.

The post-central position of the mouth, combined with the great size of the tubular pharynx, appears to have led to the modification of the originally central gut, so as to form three lobes—one anterior lying above the brain and a posterior pair, which lie at the sides of the pharyngeal pouch, and usually extend nearly to the hinder end of the body (Figs. XI., XII.); they not unfrequently unite posteriorly (cf. *Bothrioplana*). The lateral caeca may branch in the lower forms, but in the *Terricola* and *Maricola* become larger and more regular in their arrangement; but they do not appear to be so strictly metameric with nerves and gonads, as Lang (41) believed for *Gunda segmentata* and terrestrial forms (Wheeler and Dendy).

The nervous system retains to a greater extent than in the Rhabdocoelida a primitive condition, in that the brain gives origin to a number of nerve strands, which form a subdermal network all over the body; but a ventral pair of longitudinal nerves are much more prominent than the others, and connected by transverse commissures in a fairly regular way, especially in *Gunda segmentata*. But ganglion cells remain at the origin of the nerves and transverse commissures. The sense organs may be (*a*) ciliated pits at the side of the head, receiving nerves from the brain; these are especially well developed, and abundant in *Bipalium* and *Geoplana*, where they lie in a lateral groove (Fig. X 3); the former genus too has retractile papillae round the margin of the head (Moseley). (*b*) Eyes are either confined to the anterior end, or in many land Planarians along the entire margin. Dendy has suggested that the unicellular eyes (Fig. X. 2) of *Geoplana*, etc., are derived from modified rod cells; multicellular eyes occur in other terrestrial genera.

The excretory system (Fig. VII. 6) presents two laterally placed main canals which give off numerous special branches, opening dorsally on to the external surface. In *Gunda* there are two main lateral canals on each side connected by short canals, and the external pores exhibit the same repetition noticeable in other systems of organs. The main trunks are sparsely ciliated. Lang discovered in *Gunda* certain vacuolated cells with flames amongst the intestinal epithelial cells, and therefore suggests that the flame cells generally have a hypoblastic origin. It is only within recent years that the excretory system of Triclada has been described

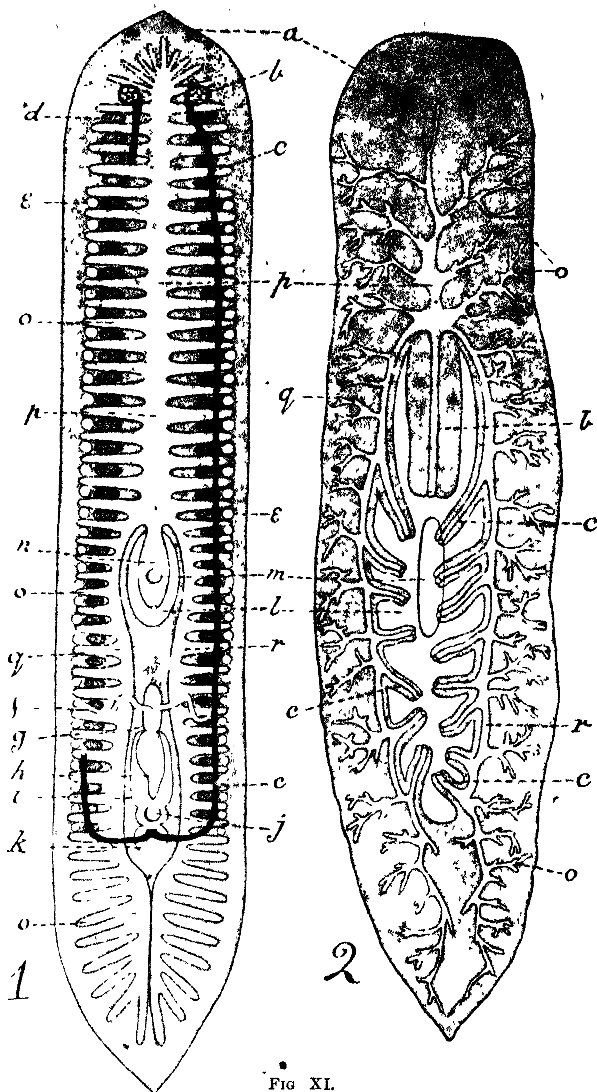


FIG XI.

1.—Diagram of the anatomy of an elongated Triclad, *Rhynchodemus* (after Moseley), in order to show the repetition of gonads and the simple character and the almost symmetrical arrangement of the intestinal diverticula with which the genital organs alternate (which are represented too symmetrical) *a*, group of eyes, *b*, germ-producing follicle of the ovary; *c*, oviduct which receives ductules from the yolk-forming follicles (*d*) when these are ripe, *e*, testes, *f*, sperm duct, *g*, seminal vesicle into which the two sperm ducts open, *h*, penis lying in the antrum masculinum (*i*), *j*, common genital pore, *k*, antrum femininum, into which the two oviducts (germ-vitellarian ducts) open; *l*, pharyngeal sac; *m*, mouth; *n*, pharynx; *p*, anterior of the three limbs of the intestine, *qr*, right and left posteriorly directed limbs of the intestine, *oo*, simple, unbranched intestinal caeca, characteristic of the Tericola

2.—Diagram of the alimentary system of *Phagocata gracilis*, Leidy (after Woodworth). *a*, eye, *b*, principal (normal) pharynx; *cc*, several accessory pharynges lying in the large pharyngeal sac (*l*), and each receiving a branch from the posterior limb (*qr*) of the intestine; *m*, *n*, *o*, *p*, *q*, *r*, as in Fig 1.

(Lang, Francotte (17), and Chichkoff (7)), and the external pores are known even now in only a few cases.

The male generative organs present further advance on that follicular arrangement which is just commencing in Alloiocoela. In the female organs the differentiation into germ-producing and yolk-producing organs, of which every stage is presented by the Rhabdocoelida, has in the Tricladida only reached half-way. In fact, we have a branched "germ-vitellarium," of which the most anterior lobe or follicle produces small egg cells, whilst the remaining follicles give rise only to yolk cells; but all these follicles open into a common "oviduct" (Fig. XII.). This organ thus differs from the "germ-vitellarium" of Rhabdocoelida, merely by being "follicular" instead of "compact." The two oviducts unite to form a shorter or longer common duct, into which numerous unicellular, albuminiparous glands pour their secretion. This region may be muscular, and is termed "vagina" In its turn it opens into the atrium genitale, which is common to both sexes. The "uterus" (Fig. XIII.), probably originally a dilatation of the lower part of the oviduct, becomes a diverticulum of the vagina (XIII. 1), (*Gunda*, *Planaria*, *Rhynchodemus Scharfi*), (cf. the accessory sac of Polyclads); or it may open into the atrium independently of the oviduct, as in various species of *Planaria* and *Polycelis* (XIII. 2); the process is carried further in *Uteriporus*, where the organ opens outside the area of the atrium, and in the parasitic *Bdelluridae* we find the same condition, but the uterus is paired (XIII. 4).

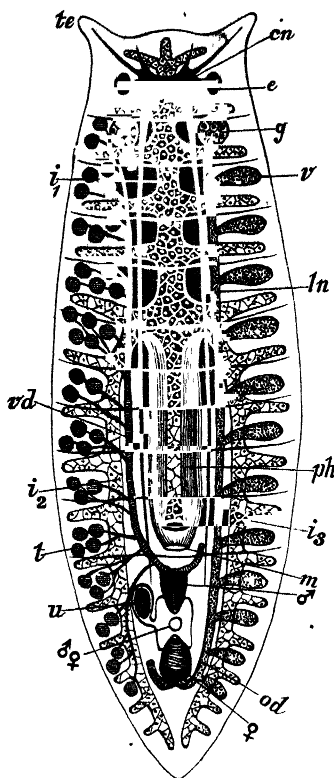


FIG XII

Plan of the anatomy of a Triclad (from v. Graff), ventral view. *cn*, brain; *e*, eye, *g*, germ-producing follicle of the ovary, i_1, anterior branch, i_2, i_3, the right and left posterior branches of the intestine; *ln*, ventral nerve, *m*, mouth; *ph*, pharynx, *od*, oviduct, *t*, testis, *te*, tentacle, *u*, uterus, *v*, yolk-producing follicles of the ovary, *vd*, vas deferens, ♂, penis, ♀, vagina, ♂♀, common genital pore.

In addition to the normal male and female copulatory organs the genus *Artioposthia* possesses elaborate accessory copulatory

organs, outgrowths of the atrial walls known as "adenodactyli" or "adenocheiri," according to their shape.

The function of the uterus (see Bergendal) appears to vary; in some cases spermatozoa are found in it (it is a spermatheca, *Bdelluridae*); in others, eggs have their cocoon deposited around them; in others, again, the cocoon is moulded in the atrium, or even in the vagina (some land Planarians), but the uterus secretes the substance which will harden to form the shell.

Development.—From four to twenty or even more egg cells are surrounded by several hundred amoeboid (v. Siebold, 1841) yolk cells in each cocoon. Each egg cell undergoes development,

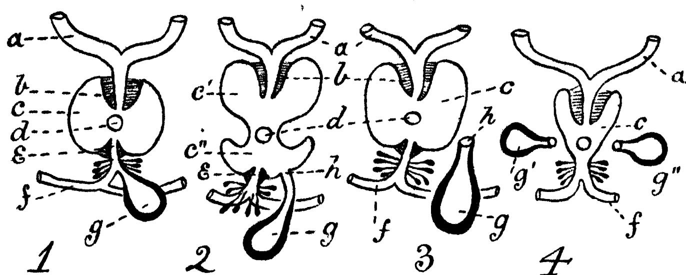


FIG XIII.—Plans of the Genital Atrium in Aquatic Triclads to illustrate the various Relations of the Uterus.

1.—*Gunda*: the uterus is here a diverticulum of the egg duct: *a*, sperm duct; *b*, penis, with ductus ejaculatorius; *c*, atrium genitale; *c'*, antrum masculinum; *c"*, antrum femininum; *d*, atrial (genital) pore; *e*, egg duct, with muscles around it, and frequently functioning as a vagina; the distal region receives gland cells, which appear to secrete the cocoon; *f*, oviduct; *g*, uterus; *h*, its opening into the atrium, or to the exterior.

2.—In *Planaria*, *Polycelis*, and many others the uterus opens into the atrium directly.

3.—In *Uteriporus* the uterus opens to the exterior by an independent pore at the side of the genital pore.

4.—*Syncoelidium* presents a pair of independent uteri (*g'*, *g"*), each opening to the exterior.

but, as in some Gastropod Molluscs and Oligochaeta, they do not all survive.

The Triclads present a very peculiar phenomenon during segmentation, in that the blastomeres resulting from the nearly regular segmentation move apart from one another (Metschnikoff, Ijima, and Hallez, 29), and lie in a fluid which appears to result from this breaking down or fusion of the yolk cells (Fig. XIV. 2, 3).

The exact details of the formation of the layers are imperfectly known; but the blastomeres become differentiated into flat epiblast cells which surround and enclose the yolk material (Fig. XIV. 4); into hypoblast cells which are arranged in two groups, while the blastocoele is occupied by wandering cells, mesoblastic in appearance, some of which give rise to additional epiblast, others to the brain, and others apparently to additional hypoblast cells; the pharynx, which is at first "simple," is employed for engulfing

yolk cells, and the embryo now becomes greatly swollen; this pharynx is, however, temporary, and disappears along with the mouth. This, perhaps, is the remnant of some larval stage, for the embryo is ciliated and moves within the cocoon. Later, a

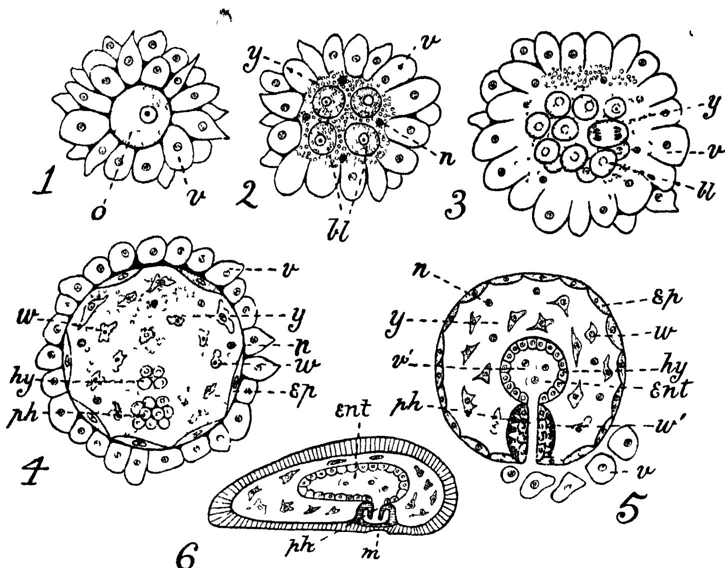


FIG XIV —The Development of *Planaria lactea* (After Hallez's figures and description)

1 —The egg cell (*o*) surrounded by some amoeboid vitelline cells (*v*)

2 —Segmentation, stage with four blastomeres, the vitelline cells are losing their independence, and are forming a syncytium, represented by the small circles (*y*), in which the blastomeres are embedded, the blastomeres (*bl*) become completely separated from one another, *n*, nuclei of yolk syncytium

3 —Later stage in segmentation, one of the blastomeres is represented in division

4 —A much later stage, showing the differentiation of the blastomeres into (*ep*) epiblast, which comes to surround the yolk syncytium, *w*, wandering cells moving in the syncytium, *hy*, a group of four hypoblast cells, destined to further subdivide and give rise to the wall of the enteron, and (*ph*) the provisional pharynx which marks the anterior end of the embryo. A few vitelline cells still remain around the embryo

5.—The cell differentiation has gone further and the epiblast (*ep*) completely surrounds the yolk syncytium (which in this figure is left plain) The four cells of the hypoblast (*hy*) have further subdivided, and now surround the enteron (*ent*) The pharyngeal cells have also undergone similar changes, and enclose a cavity communicating with the exterior, some vitelline cells (*v*) have been taken through the mouth into the enteron, and are represented by dotted circles (*v'*), some of the wandering cells (*w'*) have placed themselves round the pharynx to form its outer layer, and no doubt give rise to its muscles

6 —The embryo at a later stage changes its shape from a sphere to a flattened ovoid, the definitive pharynx is being formed from the mass of cells, and the mouth is about to form by the rupture of the lower boundary of the pharyngeal cavity From the migratory cells (*w*) will be formed the parenchymal tissue and generative organs

new mouth and a new pharynx, said to be hypoblastic in origin, replaces the temporary one. The enteron is at first rhabdocoelous, the various caeca resulting from ingrowths of connective tissue septa. Some species of *Planaria* multiply by fission, preceded in some cases (*P. albissima*) by the formation of a new head.

ORDER 3. **Polycladida**, Lang (= **Cryptocoela**, Oerst.).

Marine Turbellaria, in which the pharynx leads into a central enteron which is produced laterally into a number of caeca that may branch and extend nearly to the margin of the body. Typically this group is digonoporous.

The families may be arranged in two sections according to the presence or absence of a ventral sucker (for anatomy, etc., see Lang, 42).

SECTION A. *Acotylea.* Polycladida, without a sucker; with the mouth central or post-central; the genital pores being therefore near the hinder end of the body. If tentacles are present, they are on the dorsal surface, above the brain.

FAMILY 1. PLANOCERIDAE, Lang, with tentacles, central mouth, small stomach; penis directed backwards. *Planocera*, Blv. (Fig. XV. 1), several species are pelagic (v. Gr); *P. inquilina*, Wh., inhabits the branchial chamber of the mollusc, *Sycotypus canaliculatus* (64); *Conoceros*, Lang; *Planknoplana*, v. Gr.; *Stylochus*, Ehrb.; *Stylochoplana*, Stimp.; *Alloioplana*, Plehn.; *Plagioplana*, Plehn FAMILY 2 LEPTOPLANIDAE, Stimpson, without tentacles; intestinal caeca numerous. *Discocoelis*, Ehrb, male and female organs open by a common pore; *Cryptocoelis*, Lang, *Leptoplana*, Ehrb. (Fig. XV. 2, 3); *Trigonoporus*, Lang; *Acelis*, Plehn; *Semonia*, Plehn.; *Polyporus*, Plehn. FAMILY 3 POLYPOSTHIDAE, Bergendal (3), with several male copulatory organs. *Cryptocoelides*, Berg., *Polypostia*, Berg. FAMILY 4 CESTOPLANIDAE, Lang, elongate, without tentacles; copulatory apparatus directed forwards; *Cestoplana*, Lang; *Latocestus*, Plehn.

SECTION B *Cotylea* Polycladida, in which a sucker is developed behind the genital pores; mouth central or pre-central; genital pores just behind it. If tentacles are present, they are developed from the margin of the body.

FAMILY 5. ANONYMIDAE, Lang, with numerous penes arranged in a row along each side, but with only one female pore; mouth central; *Anonymus*, Lang (Fig. XV. 9) FAMILY 6. PSEUDOCERIDAE, Lang, tentacles in the form of folds of the anterior margin of the body; mouth pre-central. *Thysanozoon*, Grube (Fig. XVI.); *Pseudoceros*, Lang; *Yungia*, Lang; *Thysanoplana*, Plehn. FAMILY 7. EURYLEPTIDAE, Lang, mouth pre-central; pharynx tubular, directed forwards. *Prostheceraeus*, Schmarda; *Cycloporus*, Lang; one species is commensal with Polyclinid Ascidians; *Eurylepta*, Ehrb; *Oligocladus*, Lang; *Stylostomum*, Lang; *Aceros*, Lang; *Amblyceraeus*, Plehn FAMILY 8. ENANTIIDAE, v. Graff. *Enantia*, v. Gr. (23), agrees in nearly all essential features with the *Cotylea*, but is without a sucker (Fig. XV. 4, 5). FAMILY 9. PROSTHIOSTOMIDAE, Lang, body narrow, elongated; mouth far forwards; tubular pharynx. *Prosthiostomum*, Quatref. (Fig. XV. 8). FAMILY 10. DIPLOPHARYNGEATIDAE, Plehn. *Diplopharynx*, Plehn.

Further Remarks on the Polycladida.—The Polyclads are entirely marine; some attain a considerable size, viz. six inches or more; they are flat, more or less ovoid or leaf-shaped,

or more rarely elongated. They are frequently very brightly coloured.

Lang regards members of this group as representing more

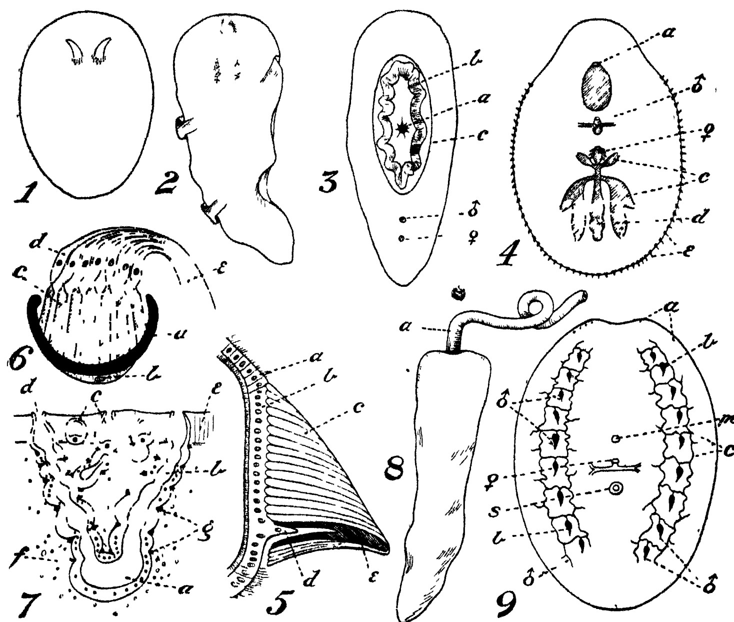


FIG XV —A Group of Polyclads (All after Lang, but 4 and 5)

1.—*Planocera graffi*, Lang , one of the Acotylea, with dorsal tentacles, and eyes at their base

2.—*Leptoplana pallida*, Lang , an Acotylean without tentacles, with a group of eye-spots above the brain

3.—*Leptoplana*, ventral view *a*, the nearly central mouth , *b*, the pharyngeal sac , *c*, the pharynx folded in the sac , ♂, male pore , ♀, female pore

4 —*Enantia spinifera*, v Gr , a peculiar Polyclad, bearing chitinous spines round the margin of the body (after v Graff) *a*, mouth , ♂, antrum masculinum, receiving the right and left sperm ducts, and opening to the exterior by the male pore , ♀, antrum femininum, receiving the uterine duct, into which open the two uteri (*c*) , it is continued backwards to form an "accessory sac" (*d*) or bursa copulatrix , *e*, the chitinous spines

5 —A section through a spine of *Enantia*. *a*, ciliated epidermis , *b*, epidermal syncytium which secretes the great basal plate of the spine, which consists of solid columns of "chitinoid substance" ; *d*, a projection of the epidermis consisting of a single cell which secretes the denser part of the spine or hook , *e*, the denser part of the spine.

6.—*Leptoplana*, section through an eye *a*, pigmented cup , *b*, nucleus of pigment cell , *c*, rods, the modified ends of nerve cells ; *d*, the nerve cells, which are prolonged into nerve fibres , *e*, the optic nerve.

7 —*Cycloporus papillosus*, Lang , horizontal section through the margin of the body *a*, a caecum giving off a couple of branches (*b*) which pass outwards to the epidermis , here each branch communicates by means of a perforated epidermal cell (*c*) with the exterior , *d*, a marginal pore The intestinal epithelial cells are indicated only by means of the nuclei, as dots , *f*, the parenchyma , *g*, groups of circular muscle fibres which constrict the caeca at intervals and give rise to the moniliform appearance of these, so usual amongst the Polyclads.

8.—*Prosthiostomum Dohrnii*, Lang. *a*, the large everted pharynx, which is exceptional in being tubular, issuing from the anteriorly situated mouth.

9 —Plan of the male organs of *Anonymus virilis*, Lang *a*, marginal eyes, extending all round the body , *bb*, the numerous pear-shaped penes and seminal vesicles arranged in two lateral rows ; the small male pore corresponding to each penis is indicated at ♂ at the point of the penis , the sperm duct (*c*) forms a ladder-like network, and communicates with each seminal vesicle. *m*, mouth , *s*, sucker , ♀, female pore receiving the uterus, right and left.

nearly than any other the ancestor of the Turbellaria, and traces the phylogeny of the Polyclads to the Ctenophora.[1]

In Lang's opinion all the constituent cells of the epidermis are embedded in a nucleated interstitial tissue deprived of cell outlines. The rod cells retain their primitive position in the epidermis (Fig. IV. 2), although in *Anonymus* rhabdites and sagittocysts are grouped to form "batteries" on the dorsal surface, which project downwards into the parenchyma (Fig. IV. 3); in this form and in *Stylochoplana tarda* true nematocysts with coiled threads occur.

The chitinous spines of *Enantia* and *Acanthozoon* (8) are specially worthy of mention. In the former they are marginal; in the latter on the dorsal surface. They suggest the chaetae of Oligochaeta on the one hand, and the cuticle of Trematodes on the other. Von Graff shows that each spine of *Enantia* (Fig. XV. 5) commences as a cuticular secretion from a number of epidermal cells raised up as a papilla; around this spine, which is hollow and golden-coloured, there are developed brownish columns of chitin (?), each column being the product of a single cell; the whole group forms a broad base to the spine, causing it to resemble the prickle of a rose tree.

In accordance with the greater size of the Polycladida, the dermal musculature becomes more complex, there being as many as six layers of alternating circular, diagonal, and longitudinal muscles, variously arranged; these, as in other forms, are more strongly developed on the ventral surface.

The parenchyma in Polycladida appears to differ from that of Rhabdocoela, in that the lacunae are intracellular, according to Lang, who has traced their development.

The mouth and pharynx may either retain the anterior position of the ancestral Platyhelminth, or by differential growth be thrust backwards to a central position, which is the more usual condition in the Polyclad; whilst in others it comes to lie near the hinder end of the body. The pharyngeal sac is spacious and the pharynx is almost universally a more or less folded, horizontal, circular sheet of muscle, which arises from the circumference of the sac (Fig. VI. 9, 12); only in the Euryleptidae and Prosthiostomidae does it take on the form of a tubular pharynx like that in Tricladida (Fig. XV. 8). The primitively simple enteron which makes its appearance ontogenetically, becomes at an early stage notched by the ingrowth of connective tissue and dorso-ventral muscles, so that a greater or less number of "caeca" are formed, and the varying extent to which this nipping takes place leads to the persistence of a larger or smaller central

[1] See Willey, *Q. J. Mic. Sci.* xl., who places *Heteroplana* n.g. in a new order Archiplanoidea, formed for the reception of *Ctenoplana* and *Coeloplana*. See Part II. of this work, "The Ctenophora," p. 16.

intestine or "stomach," from which more or less numerous caeca which may be more or less branched pass outwards towards the periphery. The caeca are arranged fairly symmetrically in pairs; and there is with a few specific exceptions always a median unpaired caecum, which passes forwards above the brain.

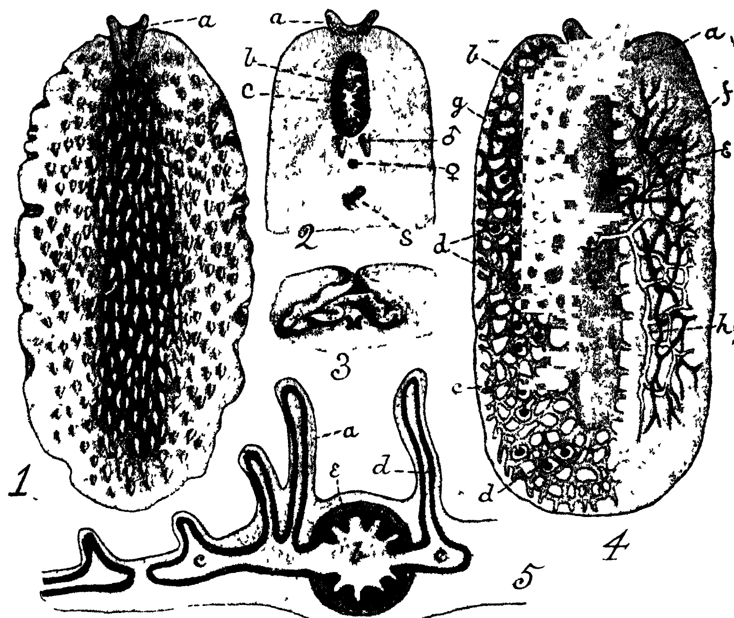


FIG XVI —*Thysanozoon brochii*, Grube (after Lang), as an Example of Cotylean Polyclad

1 —Dorsal view *a*, marginal tentacular fold The body wall is produced into a number of more or less conical papillae, each containing a caecal outgrowth of the intestine. The number of these papillae increases with age.

2 —Ventral view of the anterior end *a*, oculiferous tentacular lobes of the margin; *b*, mouth leading into the pharyngeal sac, *c*, the folded pharynx, ♂, one of the pair of penes carrying a male genital pore at apex, ♀, female pore, *s*, sucker

3.—The marginal tentacular fold of *Yungia aurantiaca*, seen from above In addition to the large pair of eyes resting on the brain, the fold is provided with numerous small eyes.

4 —Diagram of the anatomy The gut is shown only on the left side, and on the right the genital ducts *a*, brain, *b*, stomach or main gut, *c*, network of intestinal caeca, *d*, caeca entering dorsal papillae; *h*, uterus, from the network on each side a transverse branch goes to the antrum femininum, which opens by the genital pore (♀); *e*, sperm duct, forming a network, which is connected from side to side by a few transverse branches in front of ♀ pore; *f*, seminal vesicle, *g*, penis

5 —Diagram of part of a transverse section showing the main intestine or stomach (*b*) with lateral caeca (*c*) giving off the dorsal caeca (*d*) which enter the papillae (*a*), *e*, the muscular coat of the stomach.

Naturally, in the elongated forms like *Prosthiostomum* or *Eurylepta* the "stomach" becomes more tubular and the number of caeca considerable. These caeca always bifurcate and branch, and the branches may even anastomose so as to form a network in some of the Cotylea. In *Thysanozoon* and *Thysanoplana* branches from this network enter the villi on the dorsal surface, but

terminate blindly (Fig. XVI. 5); in *Yungia* some of these branches open to the exterior; while in *Cycloporus* such openings occur close together around the entire margin of the body (Fig. XV. 7). This elaborate system of caeca is no doubt intimately related to the great size of these Polycladida, for thereby nutriment is conveyed throughout the body, so that the caeca function as a lymphatic system. Nevertheless, there is but little structural difference between the caeca and the stomach, either here or in the Triclads, in which a similar process of extension, though to a less degree, has taken place. Lang regards the enteric system as homogenous with that of Ctenophora, from which he derives the group; he therefore uses the term "gastrovascular" system to indicate the stomach and its caeca. How far this is true morphologically is an open question, but to some extent the comparison is true physiologically.

The excretory system of the Polycladida is very insufficiently known; the pigmentation and large size of these forms are inimical to study in the fresh state, in which alone the excretory system can be with certainty made out; nothing, indeed, is known as to the position of the main trunks and excretory pores; all we know is that the general features of the system are similar to those of other Platyhelminth.

The nervous system appears to retain, to a great degree, certain ancestral features; it has, indeed, sunk below the epidermis and dermal musculature; but it retains the form of a close network, in which cells and fibres take a share, extending all over the body. This network, which is more strongly developed ventrally, in relation to the more muscular character of this surface, radiates from a brain which is more or less centrally situated, though in longer forms it naturally occupies a more anterior position. Only in *Oligocladus* is it behind the mouth. The nerve strands comprising the network, however, are not all of a uniform size; usually three pairs of nerve tracts are stouter than the rest, viz. a pair lying along each side of the median ventral line, a less conspicuous strand along each lateral margin, and a pair of dorsal nerves.

The eyes in this order have the same structure as in some Triclads (Fig XV. 6), but are usually very numerous; their position and arrangement are variable, and serve as useful diagnostic family and generic characters; there is always a group on the brain, usually on the tentacles; or they may lie along the margin of the body.

The genital organs attain, in the Polyclads, a more diffuse character than in the preceding orders, both male and female gonads being "follicular," and extending throughout the greater part of the body. It seems that here too, as in the case of the gut with which the organs are in close contact, this racemose

condition is related to the size of the animal; for in the smaller forms of Rhabdocoelids these organs are compact.

The male and female organs are separate throughout their entire course, there being two genital pores (the occurrence of two genital pores in marine Planarians was first noted by Mertens), the female pore being invariably behind the male (except in *Cryptocoelides*). This appears to be an ancestral character; and we have seen that it frequently occurs in the Rhabdocoelida. Though these two genital pores are usually some distance apart, they come to lie very closely together in *Stylochus*, and the region around them is slightly depressed; as this depression becomes deeper a common genital atrium is formed in *Stylochoplana agilis* and in *Discocoelis*.

The general arrangement of the male organs will be seen from the diagram (Fig. XVII.); there are one or two peculiarities in regard to the copulatory organ which may be referred to. In *Stylostomum* we have a repetition of the condition obtaining in *Prorhynchus* and *Cylindrostoma*, viz. the penis and its sac open externally in common with the pharynx and its sac.

The simplest case of duplication of penes is seen in some species of *Thysanozoon*, in which there is a pair (first recognised by Claparède) close behind the mouth (Fig. XVI. 2); whilst in *Anonymus virilis* some twelve or more pairs form a row on each side of the ventral surface; nevertheless, there is no duplication of the female apparatus (Fig. XV. 9). In *Cryptocoelides* there may be two, four, or even six penes, which, however, lie one behind the other in a common antrum. Lang has suggested that the "penis," with its glands, is developed from a simple group of glands, having originally no relations to the sperm duct; Bergendal's observations on *Polypostia* (3) seem to confirm this view. Here there is a circle of some twenty penes around the female pore, and each is traversed by a branch of the sperm duct, but the more posteriorly placed structures which resemble them in all other points are deprived of this duct; they are merely glandular. We have here, as it were, a passage from some indifferent condition of glandular organ to a specialised condition in which these glandular organs become related to sperm ducts, and therewith take on a new function.[1]

The female gonad is an "ovary," there being no differentiation to form a special yolk-producing region. The various lobes or germ-producing follicles are no doubt connected with the oviduct on each side, but such connection has not, in all cases, been traced. The oviduct on each side, or uterus, as it is sometimes called,

[1] Some interesting and suggestive facts concerning the use of the penis will be found in Whitman's paper "Spermatophores as a Means of Hypodermic Impregnation," *Journ. Morph.* iv. 1891, p. 386.

opens into a short median tube or "egg duct" with muscular walls. This duct on its way towards the exterior receives the necks of numerous glands, and this region is the "shell gland" (ootype), (Fig.

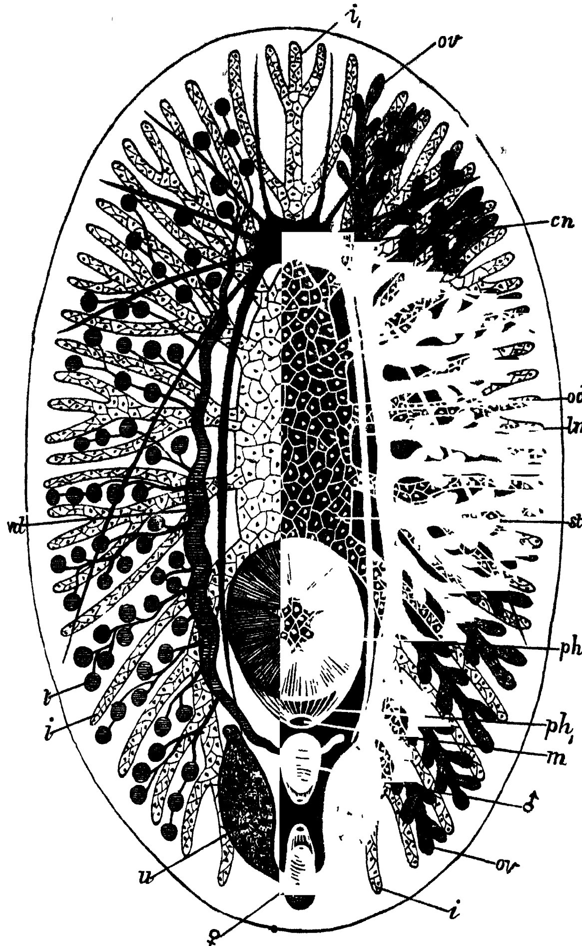


FIG. XVII.

Plan of the anatomy of a Polyclad (from v. Graff); ventral view. *cn*, brain; *i*, intestinal caeca; i_1, anterior, median, supra-cerebral caecum; *ln*, ventral nerve, *m*, mouth; *od*, oviduct, *ov*, ovary, *ph*, pharynx; ph_1, pharyngeal sac, *st*, stomach or midgut; *t*, testis; *u*, uterus, *vd*, vas deferens; ♂, penis, ♀, vagina

XVIII.); lower down the duct enters the "antrum femininum"; but in its course it, in many cases, becomes surrounded by a thick muscular sheath and then forms a bursa copulatrix (Leptoplanidae, *Planocera*, and others), and in these forms the penis is "armed."

In a number of Acotylea the egg duct is continued backwards as a blind sac beyond the point of entrance of the uterus (Fig. XVIII.); and in *Trigonoporus* this "accessory sac" effects a communication with the exterior behind the female pore (compare "Laurer's canal" in the Trematoda).

It is worthy of note that both Lang (in *Gunda*) and von Graff (in *Planocera simrothi*) have described the development of ova from the lining of the intestinal epithelium; this would go a long way in support of the very close relations between the Turbellaria and Coelentera, and of the view that there is no definite coelom in the former group, it being represented by the intestinal caeca.

Reproduction.—The eggs of the Polycladida are not laid in groups in capsules as in freshwater forms, but numbers are deposited in a jelly-like case, somewhat like the spawn of Nudibranch

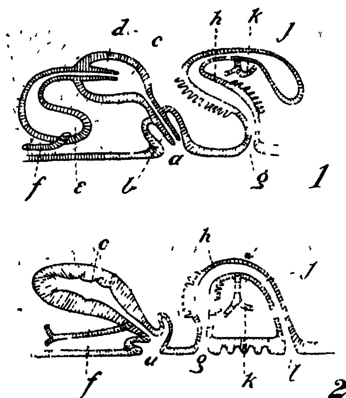


FIG XVIII

1—Diagrammatic longitudinal section of the terminal parts of the genital ducts of *Leptoplana*. *a*, male pore leading into the antrum masculinum, into which the penis (*b*) projects, *c*, vesicula granulorum; *d*, ductus ejaculatorius, *e*, the seminal vesicle, *f*, sperm duct, *g*, female pore leading into the antrum femininum, *h*, ootype surrounded by shell glands, *j*, accessory sac, *k*, oviduct

2—Similar diagram of *Trigonoporus* Letters as before Here the accessory sac (*j*) has effected a communication with the exterior (*l*), so that there are three genital pores The region of the body wall between *g* and *l* is folded, and acts as an organ of fixation (Both after Lang)

Molluscs; there is no yolk, but each egg has its own shell, which may be operculated (Fig. XIX.). Some Polyclads undergo direct development; others pass through a free-swimming larval stage, which was first noted by Joh. Muller (48).

The development of *Discocoelis* and others has been carefully worked out by Lang. Segmentation is holoblastic, but unequal, giving rise to micromeres and macromeres; the mesoblast is very early marked out as cells intermediate in size between the micromeres and the macromeres; the latter do not directly become the hypoblast, but cells free from yolk are budded off from them, which gradually surround the centrally placed yolk masses. Meanwhile, epibolic invagination has led to the formation of a definite embryo with ciliated epiblast; the central yolk masses are now devoured by the hypoblast cells, to which they stand in relation of parent to children, and the enteron gradually acquires a lumen, and effects a communication with the exterior by means of an anteriorly placed

stomodaeum, which will give rise to the pharyngeal sac and pharynx.

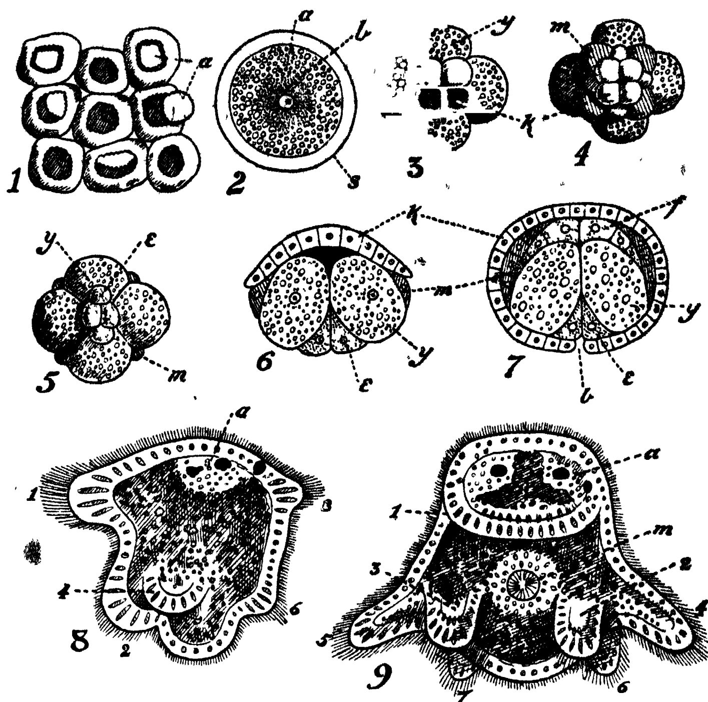


FIG XIX.

1.—Eggs of *Yungia* laid in a single sheet, embedded in jelly; each egg is provided with an operculum (*a*), which is represented in various positions, and entirely removed

2.—An egg of *Thysanozoon* *s*, the egg membrane, *a*, coarsely granular vitellus; *b*, fine granular vitellus, containing the nucleus

3, 4, 5.—Three stages in segmentation of *Discocoelis* The result of the first two cleavages is to produce four large cells, each of which then divides into a micromere (*k*) and a macromere (*y*) These first formed cells divide and the macromeres also divide, forming mesoblast (*m*). 5 represents a later stage from the opposite (ventral) pole, and shows the four primary endoderm (hypoblast) cells (*e*) derived from the four large yolk cells

6, 7.—Diagrammatic transverse sections of later stages. 6 represents the same stage as 5 The epiblast (*k*) is extending over the mesoblast, *m*. There is a small blastocoel, represented black; *e*, the primary hypoblast cells 7 is a much later stage, after the epiblast has grown right round the embryo, so as to enclose the cells, leaving however a small blastopore, *b*. In addition to the primary, ventral, hypoblast cells, others (*f*) have been formed from the yolk cells dorsally By the subdivision of these hypoblast cells (*e* and *f*), the great yolk cells will become enclosed, the nucleus is no longer distinguishable, and the yolk spherules run together to form a great homogeneous mass occupying the cavity of the gut, and serving as food The mesoblast in this stage has already extended downward for some distance.

8, 9 represent two stages in the development of the larva of *Thysanozoon* *a* is the brain with eye-spots; 1 to 8 are the eight characteristic ciliated lobes which are so well marked in Müller's larva; 1 is the median, supraoral, anterior lobe, 2, 3, the paroral lobes; 4, 5, great lateral lobes, 6, 7, pair of posterior lobes, 8, median posterior lobe

8 is a side view of a young larva. 9 is ventral view of an older layer. *m*, mouth, the light area around which is the pharynx. (All after Lang)

The embryo is now somewhat ovate; as the yolk is absorbed and the animal grows it becomes flattened, assumes the form of a young Polyclad, and leaves the shell.

In the case of metamorphic forms, the embryo, however, instead of assuming the flattened character of a Polyclad before leaving the shell, acquires eight processes of the body, arranged in a definite way round the mouth (Lang has compared these lobes and the bands of cilia upon them with the eight rows of swimming plates of Ctenophora). They constitute a preoral band, or more correctly, a circumoral band (Fig. XIX. 8, 9).

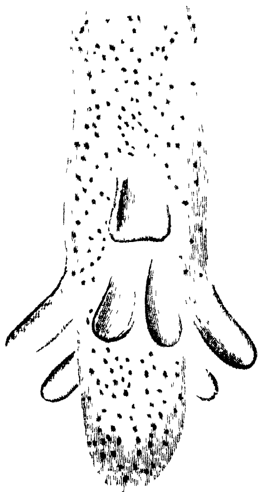


FIG XX
Muller's larva of *Yungia*, seen from the oral surface. (After Lang, from v. Graff)

This cephalotroch larva, or "Müller's larva," as it is termed (Fig. XX.), after a free swimming life, is transformed into a young Polyclad by the gradual diminution of the ciliated lobes.

The larva of *Stylochus pilidium*, owing to the great development of the dorsal surface, the unequal development of the various ciliated lobes, comes to resemble the typical Nemertine larva, "Pilidium"; and it is possible that this is more nearly like the common ancestor of Turbellaria and Nemertina, while Muller's larva has gone along a special line in the former group. Balfour showed that the trochosphere and other larval forms were readily derivable from these, which can be easily derived from a coelenterate; on this account he placed these larvae near to the ancestor of the whole group of Coelomata.

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CHAPTER XVII.

PLATYHELMIA—TEMNOCEPHALOIDEA.

CLASS II. TEMNOCEPHALOIDEA.

PLATYHELMIA, in which the flattened body is provided posteriorly with a large ventral sucker. The epidermis is retained throughout life as a nucleated syncytium, which secretes a thick cuticle, but which may also carry cilia, and contain rhabdites.

ORDER **Dactylifera.**

The body is produced into finger-shaped tentacular processes along the anterior margin or along the lateral margins as well; the mouth is situated anteriorly, and leads through a pharynx into a wide, nearly rectangular intestine, which is without diverticula. A single genital pore situated posteriorly is common both to the male and female apparatus.

FAMILY 1. TEMNOCEPHALIDAE. With four to twelve preoral tentacles. The excretory system opens to the exterior by means of a pair of anteriorly and dorsally situated contractile sacs; the vitellarium is reticulate. *Temnocephala*, Blanch. (Fig. I. 1, 6, 7); *Craspedella*, Hasw.; *C. Spenceri*, Hasw., sole species, in the branchial chamber of *Astacopsis bicarinatus*. FAMILY 2. ACTINODACTYLELLIDAE. Tentacular processes along each side of the body; a second sucker is developed in front of the mouth; no contractile sacs at the excretory pore. *Actinodactylella*, Hasw. (orig. *Actinodactylus*); *A. Blanchardi*, Hasw., on *Engaeus fossor* (Fig. I. 3).

Further Remarks on the Temnocephaloidea.—The members of this class, so far as they are known at the present day, live on the outer surface of fresh-water animals, to which they attach themselves by means of the sucker; they do not, however, feed upon the "host" but on small animals, such as Entomostraca, Rotifera, Infusoria, etc.; they can therefore scarcely be termed "ectoparasites" in the usual sense of the word. Most of the species occur on the surface of fresh-water crustacea; the Brazilian *T. Jheringii*, Hasw., in the pulmonary chamber of the mollusc *Ampullaria*, and *T. brevicornis*, Montic., on the surface of Chelonians (*Hydropsis* and *Hydromedusa*). The genus *Temnocephala* was discovered in Chili by Blanchard, who regarded it as

Annelid; and later, Philippi placed it amongst the Leeches. Thanks to the investigation of Max Weber and Haswell, we

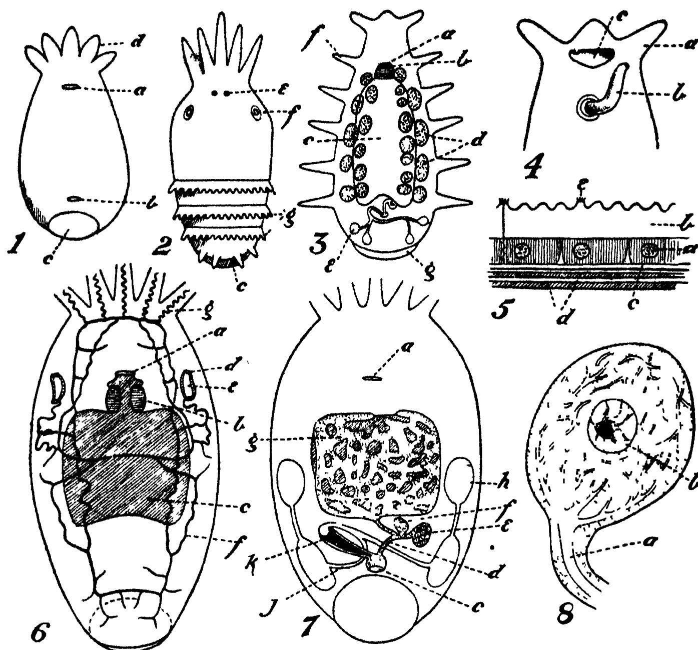


FIG 1 —Temnocephaloidea (After Haswell, and Figs 6, 7 after Weber)

1 —*Temnocephala minor*, Hasw, from the surface of *Astacopsis*, ventral view *a*, mouth, *b*, genital pore, *c*, sucker, *d*, tentacular prolongations of the body

2 —*Craspedella spenceri*, Hasw., from the branchial chamber of *Astacopsis* *e*, eyes, resting upon the brain; *f*, excretory pore and contractile sac, *g*, the three fringed lamellae on the dorsal surface, behind which are four conical papillae, *c*, dorsal edge of the sucker.

3 —*Actinodactylella blanchardi*, Hasw, from the surface of *Engaeus fossor* *a*, mouth, *b*, pharynx; *c*, intestine; *d*, follicular vitellaria, arranged along the sides of the intestine; *e*, the left testis, deeply bilobed; *f*, lateral, tentacular prolongations of the body; *g*, dorsal edge of the sucker

4 —*Actinodactylella*, ventral view of the anterior end *a*, most anterior tentacular prolongations of the body; *b*, peculiar proboscis everted through the mouth and which exists in addition to the pharynx, in which it lies when withdrawn into the body, *c*, preoral sucker.

5 —A small portion of a section through the body wall of *Temnocephala* *a*, nucleus of epidermal syncytium, which is vertically striated like the epidermal cells of *Turbellaria*, and here and there traversed by the necks of subepidermal gland cells The artist has made these too regular, so as to look like cell boundaries; *b*, cuticle raised up into low papillae, some of which bear tufts of sensory hairs (*e*), to which is seen going what appears to be a nerve fibre (on the left of the figure); *c*, basement membrane, *d*, circular muscles

6 —Plan of the alimentary and excretory systems in *T. semperi*, M Weber, as seen from the dorsal surface. *a*, mouth leading into a small pharyngeal sac; *b*, pharynx; *c*, intestine; *d*, excretory pore, *e*, contractile bladder, formed of a single perforated cell; *f*, chief excretory vessels, *g*, the vessels entering the tentacle. The outline of the sucker is indicated by dotted lines.

7 —Plan of the genital organs of *T semperi*, M Weber, as seen from below. *a*, mouth; *c*, genital pore leading into the genital atrium; *d*, oviduct; *e*, germarium, *f*, receptaculum seminis, *g*, vitellarium in the form of a network covering the dorsal surface of the intestine, *h*, the testes; *j*, sperm duct, which, after uniting with its fellow, gives rise to a seminal vesicle; *k*, penis, with chitinous sheath.

8 —One of the excretory cells of *T. fasciata*, Hasw., which exists in addition to the ordinary [illegible]e cells. *a*, tubule, branching in the substance of the cell to form a system of minute [illegible]aries; *b*, large nucleus.

know that its true position is among the Platyhelmia. It occurs in the Australian region, in New Zealand, in Celebes, Madagascar, Chili, and Brazil. The other two genera are known only from Australia.

The most interesting anatomical feature, and one which differentiates the class from the Trematoda, is presented by the external covering of the body, for the epidermis retains to a great degree its original character of a cellular layer, but the cells are not distinct; they form a syncytium, in which the round nuclei are disposed regularly (Fig. I. 5). This epidermis has, however, so far lost its original character as to be deprived of cilia in most species, and gives rise to a cuticle, varying in thickness, traversed by "pore canals" for the passage of the necks of subepidermal gland cells, which may contain rhabdites similar to those of Turbellaria. In this latter respect, then, the class resembles the Rhabdocoelida, and this resemblance is increased by the fact that in at least two species, *T. minor*, Hasw., and *T. dendyi*, Hasw., vibratile cilia have been recognised over the general body surface. The subdermal rhabdite glands form rod tracts (*Stabchenstrasse*), as in many Rhabdocoels, and are arranged in definite groups.

The tentacular prolongations of the body are peculiar to the group, though the Rhabdocoel *Vorticeros* presents two such processes. The muscular system is specially developed and modified at the posterior end to form a "sucker"; there are (*a*) fibres which pass dorso-ventrally from the body wall to the centre of the sucking disc; (*b*) dorso-ventral fibres traversing the substance of the sucker itself, (*c*) circular fibres; (*d*) radial fibres; and (*e*) certain longitudinal fibres from the ventral wall of the body into the lateral part of the sucker peduncle. By the varying contraction and extension of the muscle fibres, this sucker is enabled to attach itself firmly to any underlying surface. The possession of the sucker naturally allies the forms with the Trematoda.

The pharynx retains a somewhat primitive character in being a *Ph. bulbosus*, whose chief function is "sucking."

The excretory system of *Actinodactylella* is known only from its flame cells; but in the Temnocephalidae it presents certain peculiarities, in that the number of component cells is very few, and the nuclei of considerable size, recalling in both features the Nematode excretory system; for instance, each terminal contractile sac is formed of a single cell. In addition to flame cells of a normal structure, some of the branches of the system of capillaries terminate in large cells, one to each such branch, riddled with a number of very fine canalicules, giving rise to a structure recalling very strongly the cells of the nephridium of *Hirudo* (Fig. I. 8). The anterior position of the excretory pore, its contractile sac, the main course of the canal are features of resemblan-

the monogenetic (Heterocotylean) Trematodes, rather than with the Turbellaria.

But in the nervous system the Temnocephaloidea retain a much more primitive condition than that presented by the existing Rhabdocoelida. The extensive network arising from the brain presents three main tracts on each side of larger dimensions.

The genital organs (Fig. I. 7) are formed on the ordinary Platyhelminth plan; in their position posteriorly to the intestine, and in the lateral position of the testes, the Temnocephaloidea resemble the Turbellaria. The testes retain the primitive, bilateral symmetry; but the testis of each side is so deeply constricted as to form two oval, or it may be lobulated organs, connected together by a narrow duct, so that there is here a commencement of that process which results in the "follicular" arrangement of Tricladida, and Polycladida. The penis presents a Rhabdocoelidan character in being enveloped in a chitinous sheath, resembling that of many tubificid Oligochaetes (such as *Limnodrilus*); while the terminal region of the sperm duct is eversible, and provided with chitinous spines.

The female gonad has undergone that same differentiation into germarium and vitellarium which occurs in many Turbellaria. The former is compact; the latter presents a peculiar and characteristic arrangement in its reticulate structure, covering the dorsal surface of the sac-like intestine The vagina is armed.

The whole anatomy, therefore, of the Temnocephaloidea exhibits a remarkable intermediate condition between the Rhabdocoelida and the Trematoda, while presenting certain peculiarities of its own, which entitle the animals to a position independent of these two classes. Nothing is known of the development beyond the fact that the eggs are laid in capsules (sometimes operculated), which are pyriform and stalked, except in *T. fasciata*, where several oval eggs are embedded in a mass of secretion.

1. *Haswell.* Quart Journ Mic Sci. xxviii. 1888, p. 279.
2. *Ibid.* (For all previous literature.) Macleay Memorial Volume, 1893, p. 93.
3. *Ibid.* (Actinodactylella) Macleay Memorial Volume, p. 153.
4. *Max Weber.* Zool. Ergebnisse einer Reise in Niederl. Ost-Ind. 1890, vol. i. p. 1
5. *Plate.* SB. Akad. Wiss Berlin, 1894, p. 527.

CHAPTER XVIII.

PLATYHELMIA—TREMATODA.

CLASS III. TREMATODA (RUDOLPHI).

Order 1. **Heterocotylea.**
Fam. 1. Monocotylidae.
„ 2. Tristomidae.
„ 3. Polystomidae.
„ 4. Microcotylidae
„ 5. Gyrodactylidae.

Order 2. **Aspidocotylea.**
Fam. Aspidobothridae.

Order 3. **Malacocotylea.**
Fam. 1. Amphistomidae.
„ 2. Distomidae.
„ 3. Holostomidae.
„ 4. Monostomidae.
„ 5. Gasterostomidae.
„ 6. Didymozoonidae.

PARASITIC Platyhelmia which retain the mouth and alimentary tract of the ancestor, but in which the epidermis not only loses its cilia during embryogeny, but is apparently absent in the adult as a distinct, continuous, cellular layer, having sunk into the mesoblastic tissue, after secreting a thick, stratified, chitinous cuticle. Further, in relation to their parasitic habits, suckers are developed at or near the posterior end on the ventral surface, and also in the region of the mouth.

Historical.—Our knowledge of Trematodes begins with Gabucinus (1547), who described the occurrence of the liver fluke in sheep, which was, however, referred to by Jehan de Brie as early as 1379; Leeuwenhoek (1695) added a form found in the herring; Swammerdam (1752) mentions a distome in the frog's lung; Roesel v. Rosenhof (1758) gave a description and figure of a fluke (*Polystomum*) which he discovered in the frog's bladder. Then came t

wonderfully accurate observer, O. F. Müller (1777), who, in a series of memoirs, described a number of species, and gave good pictures of them. These earlier writers, naturally, were weak in the interpretation of anatomical features, and it has taken nearly a century since Müller's time to obtain a proper knowledge of the anatomy, while even at the present day one or two matters are open to dispute.

After Muller, the number of observers rapidly increased, and it is impossible even to mention a hundredth part of those who have aided in building up our knowledge of the anatomy and variety of forms in Trematodes and Cestodes. Max Braun (11) gives a complete list of works thereon, with a brief epitome of the contents of each memoir. The most important amongst those who have added to the number of genera and species are Rudolphi (1808), v. Baer (1827), v. Nordmann (1832), Diesing, Wagener (1858), P. J. van Beneden, Cobbold, v. Linstow, Willemoes-Suhm, Taschenberg, and in more recent times Monticelli, Sonsino, Parona, Perugia, and Stossich, as will be seen in the systematic account.

Many of the above-named zoologists naturally added to our knowledge of the anatomy and life-history of the members of the group, and the various important advances are mentioned in the text below. The following are conspicuous for the amount of new knowledge which they contributed:—Bojanus (1818), Mehlis (1825), Laurer (1830), v Siebold (1835), Leuckart, Stieda (1867), and Zeller. Carlisle (1794) deserves mention, as he appears to have been the first to demonstrate, by means of injection, the course of the canals of the excretory system which, however, he regarded as the alimentary tract.

Certain stages in the life-history of the endoparasitic forms were known in the last century, *e.g.* to Swammerdam, and some of the more important contributions are due to Nitzsch (1807), Carus (1835), Moulinié (1856), La Vallete St. George (1855), who conducted experiments in feeding probable hosts with cercariae, Pagenstecher (1857), Zeller, Schauinsland, and Thomas.

The limits of the class are very well defined, and consequently we find but few animals wrongly included therein; nevertheless, some curious mistakes have been made; for instance, Lacaze Duthiers described "Phoenicurus" as a fluke, parasitic on *Tethys;* Spengel and Bergh have, however, pointed out that it is merely a normal, readily detachable, appendage of that mollusc. "Thysanosoma," from the caecum of *Cervus dichotomus,* was at first described by Diesing as a fluke; it is really a detached proglottid of a Cestode; van Beneden included *Cyclatella,* but later recognised that it is a species of *Loxosoma* parasitic on *Clymene.* *Myzostoma* was for a long time placed here, till Leuckart

showed that it is an Annelid. While Kölliker pointed out that Cuvier's "Hectocotyle" is not a fluke, but at the same time fell into error in regarding it as a "pygmy male" of *Argonauta* and *Tremoctopus*. *Pentastoma* was included, till P. J. van Beneden (1849) discovered its embryo, and allocated it to the *Arthropoda*.

The first definite attempt to classify the parasitic worms or "Helminths," as they were then called, was made by Zeder (1800), who divided them into five families, to which he gave German equivalents of (*a*) round worms, (*b*) hooked worms, (*c*) sucking worms, (*d*) tape-worms, and (*e*) bladder-worms. Of the "sucking worms" he recognised three genera, of which he gave diagnoses, and divided the various species into groups. Rudolphi (1808), in an epoch-making work on intestinal worms, invented the term "Trematoda"[1] for Zeder's "sucking worms," which he raised to the rank of an "Order."

Both these authors laid great and deserved stress on the arrangement of the suckers, a character which, together with the absence of "segmentation," is still a sufficient mark of distinction of the Trematodes from the Cestodes.

The earlier authors were acquainted with endoparasitic forms only, and the discovery of ectoparasitic Trematodes, and the gradual increase in the number of genera and species, as well as a more correct knowledge of anatomy, due to the researches of v. Baer, Nordmann, Nitzsch, Diesing, and many others, led Leuckart (1856) to propose a division of the Trematodes into the two "families": (1) *Distomea*, for endoparasitic forms with a metamorphosis; and (2) *Polystomea*, for ectoparasitic forms which have no metamorphosis.

In the same year, Burmeister separated *Aspidogaster* from the rest, and suggested a threefold division into (*a*) *Malacobothrii* (for Distomids), (*b*) *Pectobothrii* (for Polystomids), and (*c*) *Aspidobothrii* (for *Aspidogaster*).

This system has been generally overlooked and obscured by P. J. van Beneden's great work (1858) on the group, embracing as it did not only an account of several new species, but also an experimental investigation into the life-history of the endoparasitic and ectoparasitic forms respectively; these researches led to the recognition of the importance of these two modes of reproduction: the direct or "monogenetic," and the indirect or "digenetic." And until quite recently this twofold division held the field, till Monticelli (1892) proposed the threefold division, which is essentially the same as Burmeister's.

The class Trematoda is divided into the three orders, primarily distinguished by the character of the suckers, viz.—Heterocotylea, Aspidocotylea, and Malacocotylea.

[1] τρηματώδης = pierced with holes.

ORDER 1. **Heterocotylea**, Monticelli (= **Polystomea**, Leuck. = **Pectobothrii**, Burm. = **Monogenea**, v. Ben.).

Trematoda, in which there is a large posterior, ventral, terminal adhesive organ in addition to a pair of anterior suckers in relation to the mouth; the latter may be absent. The posterior apparatus consists either of a single sucker, usually of large size, which is generally divided by radial ridges into a number of compartments; or these ridges may be so extensively developed as to give rise to a number of separate suckers set upon a caudal disc or "cotylophore." This posterior apparatus is very usually provided with chitinous hooklets.

Eye-spots are not unfrequently present. The excretory system communicates with the exterior by a pair of pores laterally placed on the dorsal surface, near the anterior end. The male and female ducts nearly always open by a common pore. A third genital duct, known as the vagina, is usually present, with an external aperture independent of the uterine pore. The members of the group are nearly all ectoparasitic, and development takes place without the intervention of an intermediate host, and without any intercalated asexual reproduction (hence "monogenetic"), so that from each egg laid only one new fluke is produced.

For accounts of the anatomy of various genera, see van Beneden, 5; Goto, 19; Cerfontaine, 14.

FAMILY 1. MONOCOTYLIDAE. Posterior sucker usually small; anterior suckers absent; the common genital pore median. *Pseudocotyle*, v. Ben. and Hesse, on skin of Selachians. *Calicotyle*, Dies; *C. kroyeri*, Dies., in cloaca of male *Raia*. *Monocotyle*, Tasch. (Fig III. 2); *M. myliobatis*, Tasch., on *Myliobatis aquila*. FAMILY 2 TRISTOMIDAE, with one large posterior sucker, with or without compartments; with or without hooklets; a pair of anterior "lateral" suckers; male and female ducts usually open by a common pore situated anteriorly, usually on the left side; vagina and its aperture single on the left side. Parasitic on gills and skin of marine fish. *Nitzschia*, v. Baer, *N. elongata*, Nitzsch, gill cavity of Sturgeon. *Epibdella*, Blv; *Phyllonella*, v. Ben. and H.; *P. soleae*, v. Ben. and H.; *Tristomum*, Cuv. (Fig. II. 1); *Acanthocotyle*, Montic.; *A. lobianchii*, Montic., on skin of *Raia clavata*. *Encotyllabe*, Dies.; *E. nordmanni*, Dies, on nostril of Bream. *Udonella*, Johnston (Fig. II. 5), on parasitic Crustacea. *Echinella*, v. Ben and H.; *Pteronella*, v. Ben. and H. FAMILY 3. POLYSTOMIDAE. The posterior adhesive organ is formed by six or eight suckers on a caudal disc or "cotylophore" which is usually armed; two anterior "buccal" suckers communicating with the oral cavity are usually present; vagina single or paired; common genital pore median. On gills of fishes, skin and bladder of Amphibia and Reptiles (see Goto, 19). SUB-FAMILY 1. OCTOCOTYLINAE, with four to eight posterior suckers; a pair of "buccal" suckers; genital hooklets. *A*. Suckers, four on each side. *Octobothrium*, Lkt.; *O. alosae*, v. Ben. and H, on gill of Shad. *Diplozoon*, v. Nordmann. The genital ducts are so arranged that the male duct of each animal ecomes continuous with the vagina of the other (Zeller, 50), or with ...lline duct (Goto, 18). *D. paradoxum*, v. Nordm., on the Minnow;

Europe (Fig. IV.). *Diclidophora*, Goto (non Diesing), (Fig. II. 4); *Dactylocotyle*, v. Ben. and H.; *Cyclobothrium*, Cerf.; *C. sessilis*, Goto, oral

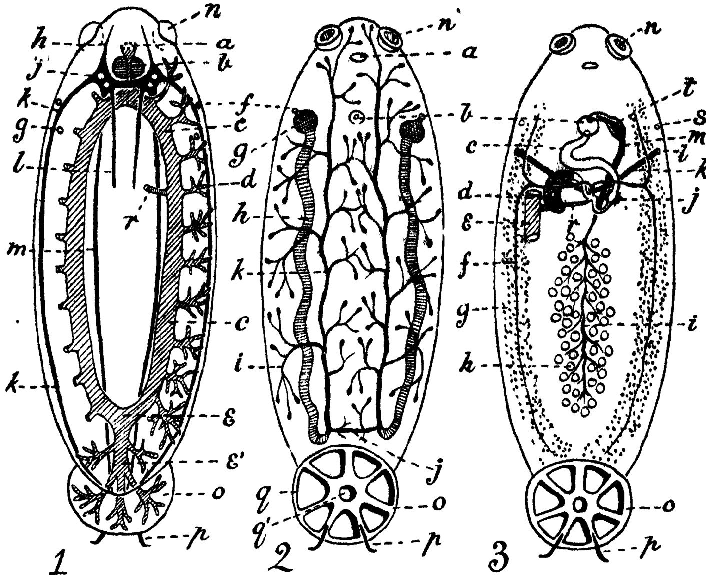


FIG I —Anatomy of a Schematic Heterocotylean.

1 —Dorsal view, showing the alimentary and nervous systems *a*, mouth, on the ventral surface, the outline being therefore dotted, *b*, pharynx, *c*, bifurcate intestine, *d*, branching, intestinal caeca, *e*, post-genital union of the two intestinal limbs, *e'*, median portion of the intestine, which is continued backwards, and gives origin to caeca in the posterior sucker (or cotylophore, as the case may be), *f*, excretory pore, right and left, situated just dorsal to the margin of the body, *g*, the vaginal pore, it is here represented as paired, but frequently it is unpaired, *h*, anterior nerve, right and left, arising from the brain, *j*, the cerebral ganglion, which carries on each side a couple of eyes, represented by white spots, *k*, marginal or lateral nerve, *l*, dorsal nerve, which is frequently present, *m*, ventral nerve The nervous system is shown in greater detail in Fig XXI, *n*, the right anterior sucker, it is unconnected with the oral cavity, and is termed "lateral"; *o*, posterior sucker, *p*, a hooklet projecting from the posterior sucker; *r*, the genito-intestinal (Laurer's) canal, entering the right limb of the intestine

2.—Plan of the excretory system, seen from the ventral surface *a*, mouth, *b*, genital pore and atrium, here represented as median, but it may lie on the left of the median line, *f*, excretory pore, *g*, contractile excretory bladder, right and left, *h*, large excretory duct, passing backwards to the hinder end of the body, *k*, the forwardly-directed (ascending) canal, in continuity with the duct posteriorly, and running to the anterior end of the body, giving off irregularly arranged branches, which subdivide to form capillaries, *i*, capillaries terminating in flame cells, which are indicated by the terminal thickenings; *j*, transverse anastomotic vessel, which is frequently present behind the genital organs, *n*, the left anterior "lateral" sucker; *o*, the posterior sucker, which is here, as so frequently, subdivided into compartments or "loculi" by radiating ridges, *p*, a hooklet, *q*, a lateral loculus, *q'*, the central loculus which may, or may not, be present.

3 —Plan of the genital organs, seen from the ventral surface, *b*, genital atrium, *c*, uterus, *d*, germarium, *e*, portion of the right limb of the intestine into which the genito-intestinal canal opens, *f*, longitudinal vitellarian duct, from each of which a transverse duct passes inwards to enter the germ duct, *g*, vitellarium; *h*, testis, consisting of a number of follicles; *i*, the sperm duct, *j*, ootype, surrounded by "shell glands", between it and the germarium is the germ duct, *k*, vagina, right and left, connected internally with the median vitello-duct; *l*, vaginal pore, *m*, the sperm duct; *n*, *o*, *p*, as before; *r*, genito-intestinal (Laurer's) canal, passing from the oviduct to the intestine, *s*, excretory pore, *t*, penis

cavity of *Chaerops japonicus*. *Heterobothrium*, Cerf.; *Vallisia*, Per. Par., *V. striata*, Per. Par., on gills of *Lichia*. *Anthocotyle*, v. Ben. and

(Fig. II. 6); *Onchocotyle*, Dies., on gills of Elasmobranchs. *B.* Suckers in a transverse row posteriorly. *Hexacotyle*, Blv. (Fig. II. 2); *H. thynni*, de la Roche. *Plectanocotyle*, Dies., has only six suckers. SUB-FAMILY 2. POLYSTOMINAE, with six posterior suckers; without anterior buccal suckers. *Polystomum*, Zeder; *P. integerrimum*, Frol., bladder of Frog and Toad (Fig. V. 1, 2; and for an account see 49). *P. ocellatum*, Rud., pharynx of *Emys europaea*. *Erpocotyle*, v. Ben. and Hesse; *Diplobothrium*, Leuckt.; *Sphyranura*, Wright; *S. osleri*, Wr., on skin of *Necturus lateralis* (see 48). FAMILY 4. MICROCOTYLIDAE, with two "buccal" suckers and numerous small posterior suckers carried on a variously

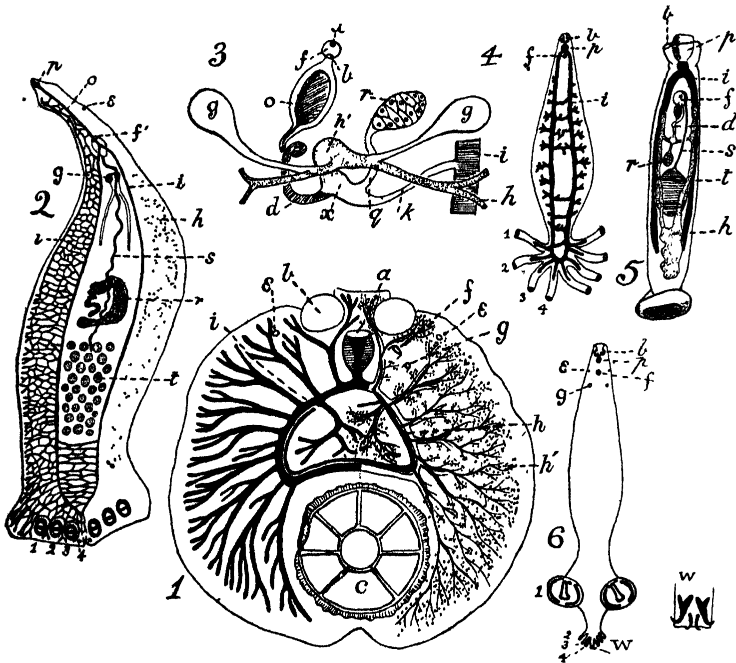


FIG II

shaped marginal cotylophore; genital pore median; vagina may open on the left side (see 37). *Microcotyle*, v. Ben. and H. (Fig. III. 1); *Gastrocotyle*, v. Ben. and H.; *G. trachuri*, v. Ben. and H., on the gills of *Caranx trachurus*. *Axine*, Abildgaard; *A. belones*, Abild.; *A. triglae*, v. B. and H. FAMILY 5. GYRODACTYLIDAE.[1] Elongated body with one or two pairs of retractile cephalic lobes, carrying the openings of glands; anterior suckers may also be present; the caudal disc does not carry suckers, but is armed with peculiar hooks, central and marginal; eyes are usually present anteriorly; genital pore median; no vagina.

[1] *Dionchus*, Goto (Journ. Sci. Coll. Imp. Univ., Tokyo, xii. 1899, p. 286), combines several characters of this and the preceding family.

Calceostoma, v. Ben.; *C. elegans*, v. Ben., on gill of *Sciaena agilis*. *Tetraonchus*, Dies., various species on other fish. *Dactylogyrus*, Dies., numerous species on fresh-water fish. *Amphibdella*, Chatin; *Diplectanum*, Dies. (Fig. III. 3); *Gyrodactylus*, v. Nordm.; *G. elegans*, v. Nordm., on gills of various fresh-water fish (see 22). The most interesting anatomical peculiarity of *Gyrodactylus* is the absence of a vitellarium, so that, alone amongst the Trematodes, the female gland is an "ovary"; this is evidently related to the peculiar mode of reproduction, the details of which are still somewhat

FIG. II.—A Group of Heterocotyleans.]

Letters common to all the figures except 3. *b*, anterior sucker, "lateral" or "buccal," as the case may be; *e*, excretory pore; *f*, genital pore, or atrium, in 5; *g*, vaginal pore, single or paired; *h*, vitellarium, or its duct; *i*, intestine; *p*, pharynx; *r*, germarium; *s*, sperm duct; *t*, testis.

1.—*Tristomum coccineum*, Cuv.; ventral view (altered from Bronn's figure). *a*, mouth, leading into the pharynx; *c*, the large posterior sucker, whose cavity is subdivided into a central and seven peripheral "loculi," by a circular and seven radial muscular ridges; a pair of small hooklets (scarcely visible in the figure) are carried by the pair of posterior radii. The intestine consists of a subcircular main canal, bearing many much-branched caeca. The canal is only represented in outline, and the caeca only partially indicated on the right of the figure. The horseshoe-shaped vitellarian duct and the branches therefrom follow the course of the corresponding parts of the enteric canal. From the anterior end of each limb of the main duct a transverse duct (represented only on the right of the figure) passes inwards to join the rest of the female apparatus, which is not represented.

2.—*Hexacotyle grossa*, Goto, from the gill of *Thynnus* sp. (ventral view, after Goto). There is a long oesophageal region (*o*) passing back from the pharynx to the level of the genital pore, behind which it bifurcates. Each limb gives rise to a series of anastomosing branches forming a marginal network shown on the left of the figure, which is continued posteriorly into the caudal disc; and behind the testes a central network is similarly formed. The pore of the vagina lies on the *dorsal* surface; the vagina itself bifurcates posteriorly, indicating its true double origin. 1, 2, 3, the three large suckers, and 4, the minute median sucker, represented by a dot on the caudal disc. Between the latter are two small hooklets, represented by short lines.

3.—The female organs of *Sphyranura osleri*, Wright, from *Necturus lateralis*, ventral view. The genital atrium (*f*) receives the male duct (*a*) anteriorly and the female duct (*b*) posteriorly; *d*, uterus, dilated distally and containing an egg (*o*) which is provided with a filament at one end; *q*, vagina, right and left, here a blind sac, having lost its external pore and functioning as a spermatheca; *h*, right and left, transverse vitelline duct; *h'*, yolk reservoir (?=ootype); *i*, portion of the intestine; *k*, genito intestinal canal; *q*, germ duct; *r*, germarium; *x*, the point of union of the various ducts.

4.—*Diclidophora elongata*, Goto, showing the alimentary system. The two limbs of the intestine are united by several transverse branches, both in front of and behind the genital organs (which are not represented). Caeca are also given off laterally, and one enters the stalk of each posterior sucker. 1, 2, 3, 4, the four suckers at the left side, each is armed and pedunculated.

5.—*Udonella caligorum*, Jnstn., from *Caligus* (after P. J. van Beneden). *b*, the anterior sucker surrounds, as by a collar, the everted pharynx. The posterior sucker is a simple deep cup. The uterus contains an egg anteriorly. The right and left lobes of the vitellarium are united posteriorly by a median lobe. The transverse vitellarian ducts are seen passing to the ootype, which receives also the germ duct from the germarium. The intestine, here, is a simple bifurcated tube, without caeca.

6.—*Anthocotyle merlucii*, v. Ben. and Hesse, from the gill of *Merlucius vulgaris* (after Cerfontaine). Outline showing the ventral surface, pores, and suckers. 1, the large clasping sucker of the posterior system, one valve alone, with its armature, is shown; 2, 3, 4, the three small suckers; *w*, the terminal region of the disc (enlarged on the right), with its two pairs of hooklets.

obscure. A single egg ripens at a time, and develops into an embryo while in the uterus; but within this embryo a second embryo becomes marked out before the first leaves the mother (Fig. III. 6). There are thus three generations, one within the other; and Wagener (46) has suggested three possibilities to explain what happens, but is unable to decide between them. (*a*) The grand-daughter arises, like the daughter, by the ordinary sexual process (which is very improbable). (*b*) Some of the blastomeres of the original egg remain quiescent and take no share in the formation of the daughter, but later undergo development within it to form the second

embryo ; in this case the two are sisters. (*c*) The second embryo, or third generation, is a "spore."

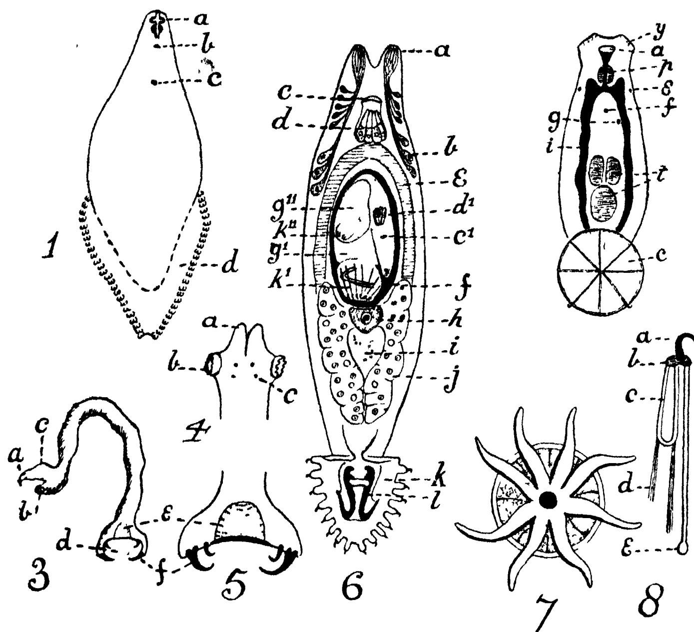


FIG III —Heterocotyleans

1 —*Microcotyle fusiformis*, Goto, from the gill of *Centronotus rubulosus* (ventral view, after Goto) *a*, buccal suckers opening into the oral cavity, behind which is the pharynx, *b*, common genital pore, *c*, vaginal pore, *d*, the lateral cotylophore with numerous small suckerlets, each armed with chitinous skeleton

2 —*Monocotyle ijimae*, Goto, from the oral cavity of *Trygon pastinaca* (ventral view, after Goto) *a*, mouth, *c*, one of the eight compartments or loculi of the posterior sucker, which is provided with a pair of small hooklets inserted in the hindmost pair of radii, *e*, excretory pore of the left side, *f*, common genital pore, *g*, vaginal pore, to the left of the middle line, *i*, intestine, *p*, pharynx, *t*, testis, here divided into three lobes, *y*, the "sticky glands," which functionally replace the anterior suckers

3 —*Diplectanum aequans*, Dies (side view after v Beneden) *a*, the anterior end bilobed and carrying a hook, *b*, the left anterior, lateral sucker, *c*, eye-spots, *d*, great posterior sucker armed with large hooks, *e*, the rows of small spines in the wall of the sucker, *f*, hooks

4 —The same, anterior end, dorsal surface *c*, eye-spot

5 —The same, posterior end, letters as before

6 —*Gyrodactylus elegans*, v Nordm, from gills of various fresh-water fish (after Wagener); ventral view. *a*, anterior lobe of the body which carries the pores of the "sticky glands" (*b*); *c*, the mouth, *d*, pharynx, lying in the pharyngeal sac, the pharynx is eight-lobed, and each lobe consists of an anterior clear portion and a posterior granular portion; *e*, the intestine, c', mouth of first embryo, d', the pharynx of first embryo, *f*, uterus, with two embryos, one within the other, g', the first embryo, g'', the second embryo within the first; *h*, egg in oviduct, *i*, testis; *j*, ovary, *k*, caudal disc, the margin of which is provided with a number of papillae, each of which carries a hooklet; *l*, the great central hooks of the disc, k', the caudal disc of the first embryo, k'', the same of the second embryo

7.—The same, the everted pharynx seen from below, showing the eight tentacle-like processes diverging through the oral aperture, the black centre is the entrance from the pharynx to the cavity of the intestine, the granular part of pharynx is not everted

8 —The same, one of the marginal hooks *a*, the free end of the hook, *b*, the plate to which the handle *e* is inserted; *c*, the hoop which serves for the attachment of muscles (*d*)

Metschnikoff (34) has made an interesting comparison with the normal development of *Monostomum mutabile* and other Trematodes. The result

of segmentation in these is a blastosphere in which the outer layer of cells becomes ciliated while the central mass becomes the "sporocyst." He suggests that the first embryo of *Gyrodactylus* or daughter may be compared with the former, the grand-daughter with the latter, as they are both formed from a mass of embryonic cells which separate in the same way as in *Monostomum*, whilst v. Linstow (1892) has suggested that *Gyrodactylus* is a larval form capable of reproducing by an asexual method.

Remarks upon the Order Heterocotylea.—The general anatomy of the group is sufficiently evident from the figures, and will be treated, together with that of the Malacocotylea, later (p. 77).

Reproduction.—The life-history forms an important distinctive character of the order. The only observed instance of copulation is that of *Polystomum* (Zeller, 49), which is temporary, and the permanent copulation of two *Diporpae* (Dujardin), which was shown by v. Siebold to form that anomalous animal *Diplozoon.*

From the fact that many of the Heterocotylea live isolated on the gills of fishes, and that eggs are laid by them, it is probable that self-fertilisation occurs; this is borne out by observations on *Distomum, spp.* by Looss (31), who finds spermatozoa within the uterus before the external pore is formed. They could therefore only have been derived from the ripe male organs; and further, in some species there is no penis, so that copulation could not have taken place. If self-fertilisation may occur in *Distomum*, there is every reason to expect its occurrence in the Heterocotylea.

Each egg, when laid, consists of a single germ cell, derived from the germarium, embedded amongst a considerable number of vitelline cells (yolk cells) derived from the vitellarium, as in Triclads, and surrounded by a shell, which is secreted by the walls of the "ootype." The form of the egg, which is frequently of systematic value, depends upon the shape of the "ootype." The shell is provided with an anterior operculum. The shell substance is produced into a filament at one or both ends; that arising from the body of the shell—the "stalk"—is used for attaching the shell to the host.

Rarely (*Polystomum*) the eggs are laid in the water. Practically nothing is known of the segmentations and early stages in development in the Order, though Zeller has described the course of events in *Polystomum.* The egg cell becomes multinucleate before cell division takes place; ultimately a solid blastosphere is formed. The yolk cells, meanwhile, become reduced in size; and as the growing embryo absorbs more and more of the yolk, the yolk cells become broken down, and finally, when the embryo acquires a mouth, the remains are swallowed. When hatched, the larva swims freely in the water by means of five incomplete girdles of cilia, of which the three anterior are incomplete dorsally, the two posterior incomplete ventrally (Fig. V. 5, 6). Posteriorly the body is produced into a caudal disc, armed with sixteen hook-

lets, but without suckers. The larva possess four eyes, an intestine, and a well-developed excretory system. During its passage through the water, the larva seeks for a young tadpole of the frog, and not

FIG IV.

finding one within twenty-four hours, the cilia degenerate and the animal dies. But having come across its future host, it swims and creeps leech-like over the surface of the body till it arrives at the branchial aperture; into which it darts with great suddenness.

Arrived in the gill chamber, the larva undergoes a gradual metamorphosis, the cilia disappear, and the cells bearing them shrink up; suckers make their appearance in pairs on the caudal disc, each being formed around a hooklet, thus leaving ten hooklets outside the suckers. Meanwhile, the tadpole itself is undergoing metamorphosis, and the young *Polystomum* makes its way into the pharynx, and wanders along the alimentary tract to the rectum; on the formation of the cloacal bladder, the young *Polystomum* enters it. It is not till the third year that the parasite becomes sexually mature. But if, as sometimes happens, the larva of the parasite has attacked a younger tadpole than usual, one in which the external gills are still present, it can

FIG. IV.—*Diplozoon paradoxum*, v. Nordm., from the Minnow. (Figs. 2-8 after Zeller.)

1.—The complete animal pair (altered from v. Nordmann) seen from the ventral surface. The individual *AA'* is permanently copulating with *BB'*. The intestine is shown in each; it consists of a single tube produced into caeca, really on all sides, but appearing here only on right and left. Beyond the point of union of *AA'* with *BB'*, and in the region occupied by the genital system, their lateral caeca are absent, but they reappear again behind the testes. In *D. nipponicum* the intestine bifurcates at the cross and surrounds the genital organs, behind which the two limbs again unite. *q*, caudal disc, with four suckers upon it.

2.—A pair enlarged to show the genital organs. *AA'* is seen from the ventral surface; *BB'* is truncated, and seen from the dorsal surface. *a*, the mouth; *b*, buccal sucker; *c*, pharynx; *d*, intestine; *e*, vitellarium of *AA'*; *f*, vitelline duct; *f'*, its dilated region in the tail; it enters the germ duct just beyond the origin of the "vagina"; *g*, testis of *BB'*; *h*, sperm duct, which can be traced forwards into the anterior part of the animal, curves round and communicates with the vagina (*i*) of *AA'*, which is seen passing ventrally below the germarium. *k*, the germarium, the hinder end of which is produced into the transversely disposed germ duct which receives the vagina and vitelline duct, and is continued forwards to form the uterus (*l*). The enlarged part (*l'*) of the uterus is lined by large cells; the anterior part, which runs transversely, is termed by Zeller "egg duct"; it opens to the exterior at (*m*) the female pore situated on a slight papillae and communicating with *l* by a narrow duct *n*. *p*, the caudal disc, dorsal surface in *B'*, bearing below it (in *A'*) the four suckers (*q*), each of which is armed.

3.—An egg shell. *a*, operculum; *b*, filament.

4.—Young ciliated larva. *b*, buccal sucker; *c*, pharynx; *d*, intestine; *q*, the most anterior sucker, the only one yet developed.

5.—Older larva, after the loss of cilia, and now known as *Diporpa*. On its ventral surface a special sucker (*e*) has developed.

6.—Two Diporpae about to unite. The ventral sucker of *A* is seizing the dorsal papilla (*f*) of *B*.

7.—The two Diporpae are twisting round, so that the ventral surfaces of the "tails" are towards each other.

8.—The two Diporpae have arrived at the definitive position, forming a cross, and constituting a *Diplozoon*.

obtain so copious a supply of nutriment that it grows extremely rapidly, and produces eggs in five weeks; it remains, however, in the gill chamber when this is formed, and dies before the metamorphosis of its host. Thus "gill parasites" differ in several points from the "cloacal form," notably in the absence of a vagina, and consequently in the impossibility of copulation.

ORDER 2. **Aspidocotylea**, Monticelli (= **Aspidobothrii**, Burm.).

Trematoda in which the adhesive apparatus has the form of a great sucker occupying nearly the entire ventral surface of the body, from which it is usually distinctly constricted off. This single sucker becomes, during development, traversed by transverse (and usually also longitudinal) ridges, and is thus in the adult subdivided into a number of more or less

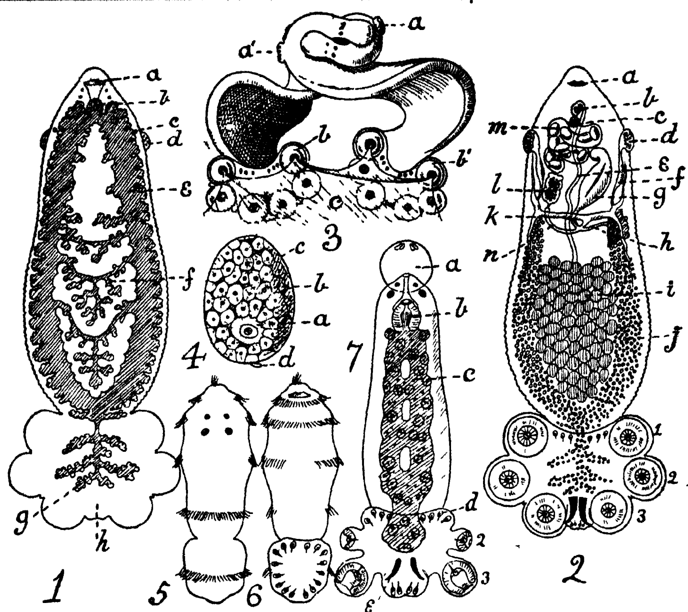


FIG V —*Polystomum integerrimum*, Fröl, from the Cloacal Bladder of the Frog (After Zeller, but 5, 6 partially original)

1.—Dorsal view, showing the alimentary tract *a*, mouth, *b*, pharynx, between *a* and *b* are the four eyes which are very small in the adult, *c*, excretory pore of right side, *d*, vaginal pores on the "lateral swelling" of the right side, *e*, the right limb of the intestine, *f*, the transverse anastomoses, *g*, the prolongation of the median gut into the caudal disc, *h*, caudal disc or cotylophore

2.—Ventral view, showing the reproductive system *b*, penis, *c*, common genital pore, *e*, sperm duct, *f*, vaginal canal, dilated to form a spermatheca, *g*, germarium, *h*, the genito-intestinal canal, passing from the oviduct to the left limb of the intestine, a small piece of which is shown, *i*, testis, *j*, vitellarium, extending into the caudal disc, *k*, vitello-duct, the index line passes to the point where the fore and aft longitudinal ducts unite to form the transverse duct, from the middle of which a short nearly median duct passes to the oviduct, *l*, ootype, containing an egg cell, surrounded by vitelline cells, the shell glands around the ootype are not shown, *m*, uterus, short and slightly undulating, containing a small number of eggs, *n*, the germ duct On the caudal disc are the three suckers (1, 2, 3) on each side, each surrounding a small hooklet (cf Figs 6, 7) Six small hooklets are visible between the anterior pair of suckers, and four others, as well as two large hooks, lie between the posterior pair of suckers

3 —Two individuals copulating The genital pore of each is placed in contact with the right "lateral swelling" of the other, the left lateral swelling of each is indicated by *a* and *a'* By means of the suckers *b*, *b'*, each individual is attached to the wall of the cloacal bladder, a portion of which is represented at *c*, and being transparent, allows the six suckers of each animal to be seen through

4 —An egg, *a*, the germ cell, *b*, vitelline cells, *c*, egg shell, *d*, the "stalk"

5 —A larva, seen from the dorsal surface, the eyes, ciliated bands, and apical tuft of cilia are shown

6 —A larva, from the ventral surface. The caudal disc at this stage is without suckers, but is armed with sixteen hooklets

7 —A young *Polystomum*, in which the two hindmost suckers (2, 3) on each side have made their appearance. The first to appear is No 3, each is developed round a hooklet, they are here seen in optical section, as the young worm was much stretched, *e*, the pair of great hooks have made their appearance in the middle of the posterior region of the disc The most anterior sucker on each side will develop around the hooklet lying just behind that labelled *d* The pharyngeal sac is everted (*a*) during the movement of the worm, and in its endeavours to find a resting-place, *b*, pharynx; *c*, sac-like intestine, beginning to exhibit central interruptions, which in the course of development are destined to increase in size, while the transverse anastomoses will proportionately diminish The circular marks represent large cells which, during the course of metamorphosis, accumulate brown granules and concretions, and then drop off into the gut.

rectangular compartments (suckerlets). There is no anterior sucker related to the mouth. The intestine is a simple sac like that of the Rhabdocoele Turbellarians, and is entirely deprived of lateral caeca.

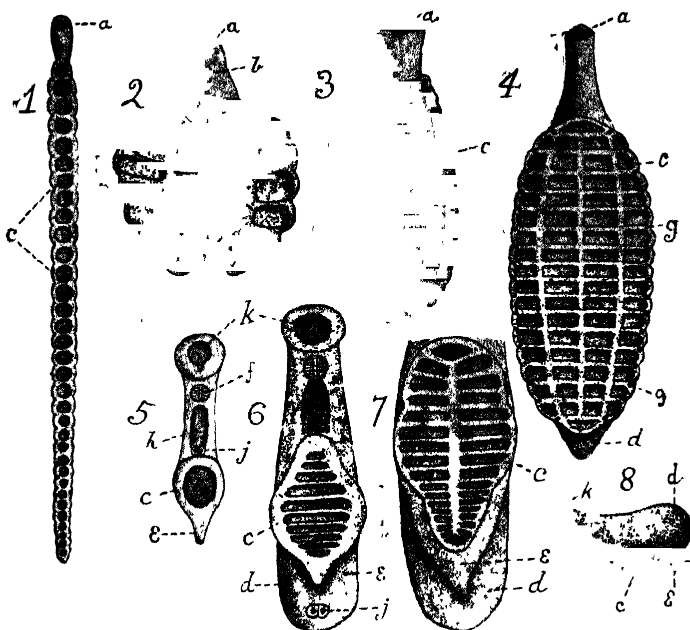


FIG VI —Aspidocotylea

1 —*Macraspis elegans*, Olss, from the gall-bladder of *Chimaera*. (Altered from Monticelli)
2 —*Platyaspis lenoiri*, Poir (After Monticelli) From the intestine of the Chelonian, *Tetrathyra vaillanti*, from Africa
3 —*Cotylogaster michaelis*, Montic., from the fish *Cantharus vulgaris* (Altered from Monticelli)
4 —*Aspidogaster conchicola*, v Baer, from *Anodon*, etc (After Monticelli) *g*, the marginal sense organs of the sucker
5, 6, 7 —Three stages in the development of *Aspidogaster* (After Voeltzkow) In the youngest freshly hatched embryo (5) the sucker is posterior and simple, the mouth is provided with an oral sucker In a later stage (6) the hinder end of the body has grown backwards, thrusting the posterior sucker on to the ventral surface, the sucker itself has increased in size, and a series of transverse muscular ridges has developed, dividing its cup into a series of compartments, the contractile sacs (*j*), which are at first apparent anterior to the sucker, having during the process of growth been carried backwards beyond the hinder margin of the sucker In a later stage (7), of which only the posterior end is shown, the process has gone still further, a median ridge now divides each of the compartments into two. By the appearance of a right and left lateral ridge the adult condition is brought about
8 —Side view of an embryo at about the same stage as 5
The following letters have the same signification throughout.—*a*, mouth; *b*, genital pore; *c*, ventral sucker; *d*, post-acetabular portion of the body in *Aspidogaster*, *e*, the curious tongue-shaped prolongation of the sucker of the embryo, which ultimately disappears as the sucker enlarges; *f*, pharynx, *g*, marginal sense organs in *Aspidogaster*, *h*, intestine, *j*, the pair of contractile sacs, each with a concretion, these sacs are the forerunners of the dilated portions of the collecting tubes (*b* in Fig VIII) of the adult.

Development is direct; there is no ciliated larva; there is no intermediate host (see 35, 41, 44).

FAMILY—ASPIDOBOTHRIDAE, Burmeister. The single family has the

characters of the order. *Aspidogaster*, v. Baer, in Mollusca. *Platyaspis*, Montic., in Chelonians. *Cotylogaster*, Montic., in *Cantharus vulgaris*. *Macraspis*, Ols., in gall bladder of *Chimaera*.[1]

Further Remarks on the Order Aspidocotylea.—The members of this group agree in their life-history with the monogenetic Heterocotylea, but structurally they are more closely related to the Malacocotylea, especially in the arrangement of the excretory and the reproductive organs, as well as in their endoparasitic habit. In their young condition, with a small posterior, ventral sucker and an anterior oral sucker, *Aspidogaster* very closely resembles *Distomum*. The form of the alimentary canal and details in the generative organs are, however, peculiar to the order. It has been by some authors grouped with the Heterocotylea (Monogenea), by others with the Malacocotylea (Digenea).

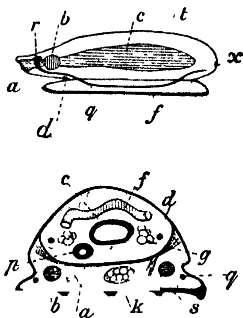


FIG VII.—*Aspidogaster*

The upper figure represents a side view of the animal *a*, mouth, *b*, pharynx, *c*, intestine, *d*, genital pore in the cervico-pedal pit (of Stafford), *f*, foot carrying the sucker, *q*, ventro-lateral nerve; *r*, cerebral ganglion, *t*, body, *x*, excretory pore

The lower figure is a diagrammatic transverse section, at about the level of the germarium *a*, the horizontal muscular septum dividing the body cavity—filled of course with parenchyma—into an upper chamber, and a lower, and extending from the genital pore to the hinder end of the intestine, *b*, the collecting vessels of the excretory system, *c*, intestine, *d*, excretory tubule, *f*, uterus, *g*, vitellarium, *k*, germarium, *p*, penis, *q*, longitudinal nerve in the foot, *s*, sucker showing the three ridges and the margin

But Burmeister first, Monticelli more recently, have erected a special order for it and its allies.

Aspidogaster conchicola, v. Baer, is a small organism occurring in various species of *Unio* and *Anodon* of Europe and North America. According to Voeltzkow it infests several organs, but most frequently (66%) Keber's red-brown organ; less frequently (33%) the pericardium, and very rarely the organ of Bojanus; whilst in the young stages it is parasitic in the intestine. It also occurs in some fresh-water Gastropods.

The general shape of the animal, with its neck, body, and central sucking disc, recalls strongly that of some Gastropod mollusc (Fig. VII.). The general anatomy will be gathered from the diagrams (Fig. VIII.); it is a form comparatively easy to obtain and to study.

[1] It is probable that *Stichocotyle*, Cunningham, belongs to this family, rather than to the Holostomidae (see 36). It is only known in an immature condition encysted in the wall of the intestine of *Homarus americanus* and *Nephrops norvegicus*. Monticelli also includes *Aspidocotyle* in this order.

The simple and archaic character of the intestine appears to be related to the exceptional dorso-ventral thickness of the body, for

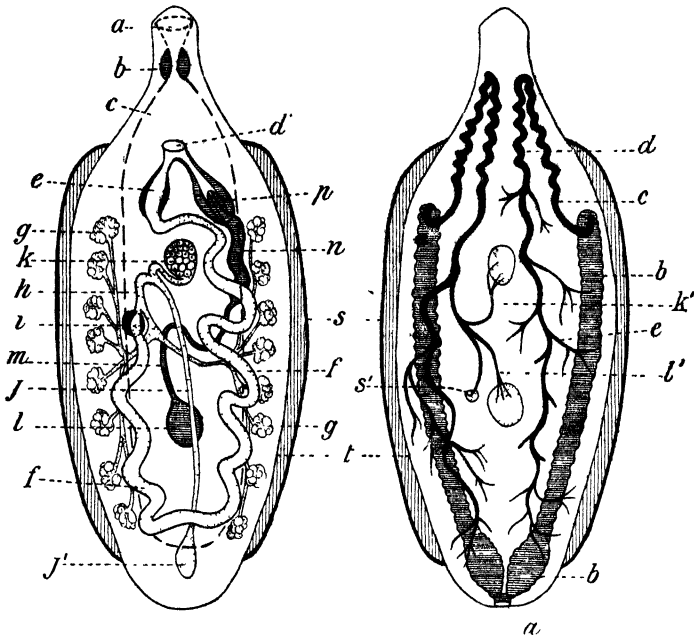


FIG. VIII —The Structure of Aspidocotylea, founded on that of *Aspidogaster*

On the left, plan of the generative organs, seen from above The alimentary canal is indicated by dotted lines, in order to illustrate the dorsal position of the uterus throughout the greater part of its extent, and its passage round the sides, to gain the ovary on the one hand and the genital pore on the other *a*, mouth, *b*, pharynx, *c*, the simple sac-like intestine; *d*, genital pore (really ventral in position) leading into the genital atrium, *e*, the copulatory region of the uterus surrounded by glandular tissue, *f*, the uterus, long, undulating, as in a Distome, and dorsal in position, *g*, vitellaria, with a longitudinal duct on each side connected by a transverse vitelline duct to open by a short common duct into the germ duct (*h*), *i*, ootype, surrounded by the shell gland, *j*, Laurer's canal (=recept vitelli of Voeltzkow), arising from the germ duct and passing backwards to terminate in a pyriform dilatation (*j'*) just below the skin of the dorsal surface, immediately behind the end of the intestine, *k*, germarium, *l*, testis, here a single "compact" organ, *m*, sperm duct, *n*, seminal vesicle, *p*, penis, surrounded by prostate gland, *s* is the outline of the sucker which just projects beyond the margin of the body; *t*, outline of body

On the right, plan of the excretory system *a*, excretory pore (there are two, according to Stafford), *b*, the great collecting vessels or ducts dilated posteriorly to form a bladder; *c*, excretory tubule arising from its anterior end and passing into the neck; *d*, the recurrent limb; from the point marked by the index line there are, in the whole course of the system, bunches of cilia (flames) set close together along the mesial wall of the tubes. This main tube gives off branches (*e*) which, according to Stafford, always came off in 3's, and the subsequent branching is also in 3's, after six such trifurcations the finest capillaries terminate in flame cells. This figure was drawn before Stafford's paper appeared, and is schematised from Voeltzkow's side view, he, like Huxley, described the right and left canals as asymmetrical, as here represented; Stafford believes them to be symmetrical, *k'*, the branch from left canal to the germarium; *l'*, the branch to the testis; *s'*, the branch to the sucker, according to Stafford, similar branches issue from the right canal as well.

the reproductive organs can attain their full size and development without compressing the gut and interfering with its primitive sac-like form. The wall of the intestine, as well as that of the

wide collecting canals of the excretory organs, is provided with distinct layers of circular and longitudinal muscles—an unusual condition amongst the Trematoda.

The retractile sense organs arranged at definite intervals along the margin of the ventral disc are extremely peculiar; they are supplied by a special nerve traversing this margin.

The body is divided into an upper and a lower portion by a horizontal muscular partition (Fig. VII.), extending anteriorly from the genital pore as far backwards as the end of the intestine; in the dorsal portion are situated the intestine, the terminal portions of the genital ducts, and the vitellaria; whilst in the ventral portion lie the gonads, the wide excretory canal, and the lateral nerves.

With regard to the reproductive organs, the single globular testis is exceptional, retaining the ancestral form. Certain parts of the female apparatus are difficult of interpretation; the *receptaculum vitelli* or *receptaculum seminis* is now regarded as homologous with "Laurer's canal," which has lost its external opening (Looss, Goto). It is stated to contain yolk spheres, and is developed by proliferations of epiblast cells from the dorsal surface (44). Self-copulation has been directly observed by Voeltzkow, and no doubt constantly occurs, as frequently only a single parasite is found.

The egg develops into a young embryo, which differs from the adult, chiefly in the fact that the sucker is posteriorly placed on the ventral surface, and is relatively small (Fig. VI. 5-8). There is also an oral sucker. The posterior sucker gets carried forwards by the growth of the hinder dorsal part of the body; and the gradual formation of the compartments has been observed.

The mode of infection is unknown, since the embryos have only been hatched artificially, and it is unknown whether eggs or embryos leave the body, and how they arrive in the organs in which they are parasitic.

ORDER 3. **Malacocotylea**, Monticelli (= **Distomea**, Leuck. = **Malacobothrii**, Burm. = **Digenea**, v. Ben.)

Endoparasitic Trematoda in which the suckers are never more than two in number, viz. a circumoral sucker, and a second, somewhere on the ventral surface; the latter may, however, be absent. In addition to these two typical suckers, accessory organs are developed to aid in fixation, in the form of glandular papillae, or scattered spines; but there are never any hooklets or skeletal pieces on the chief ventral sucker. The two forks of the intestine are usually without caeca. The excretory system always opens to the exterior by a median posterior pore which leads into a median contractile sac. In addition to the pores of the sperm duct, and uterus, which normally open through a common atrium,

there is usually a small aperture on the dorsal surface which leads into a narrow canal, known as "Laurer's canal," opening into some part of the female duct system. There is never a separate vagina in the sense in which the word is used in the Heterocotylea.

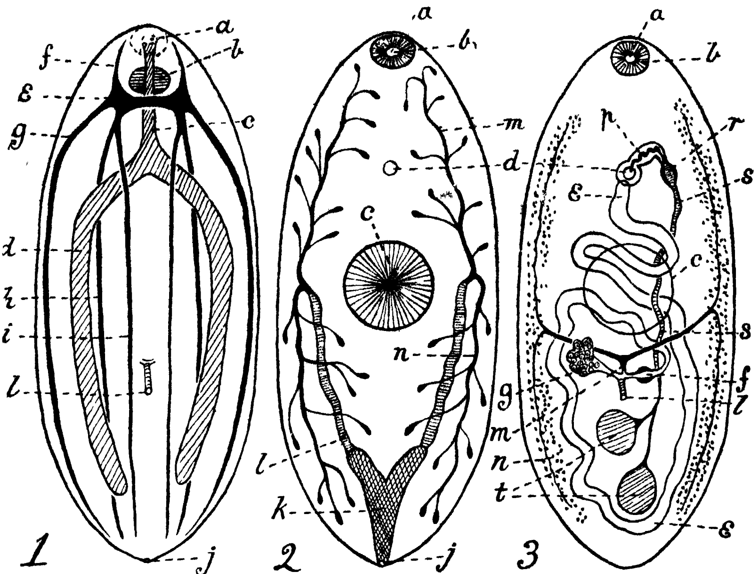


Fig IX —The Structure of a Schematic Malacocotylean (Founded on that of a *Distomum*)

1 —Plan of the alimentary canal and the nervous system, supposed to be seen from the dorsal surface *a*, the ventrally placed mouth (represented by dotted outline) lying in the centre of the anterior sucker, also indicated by dots, *b*, pharynx, *c*, median portion of the intestine (this may be long or so short as to be practically absent), *d*, the bifurcate intestine which typically is without caeca, *e*, the brain, *f*, anterior nerve, *g*, marginal (lateral) nerve, *h*, the ventral nerve, *i*, the dorsal nerve stem (the commissures are not represented, see Fig. XX.), *j*, the posterior, median excretory pore, *l*, the dorsally placed aperture to which Laurer's canal is seen passing upwards

2 —Plan of the external anatomy of the ventral surfaces and of the excretory system *c*, posterior or ventral sucker, *d*, the genital pore, *j*, the excretory pore leading into a median contractile bladder (*k*) which bifurcates anteriorly and receives on each side the duct or collecting canal (*l*), this runs forward to a varying distance and then gives rise to two canals—(*m*) the anterior and (*n*) the posterior canals, each of which gives off branches terminating in flame cells

3 —Plan of the genital organs supposed to be viewed from the ventral surface. *c*, margin of the ventral sucker, *d*, genital pore leading into the genital atrium and receiving the male and female ducts, *e*, uterus, long and undulating, *f*, ootype, surrounded by the shell gland; *g*, germarium The region between *f* and *g* is the germ duct, and receives on one side Laurer's canal (*l*), and on the other the median vitello-duct (*m*), *n*, the vitellarium, with longitudinal vitello-duct connected by transverse ducts to the median duct; *p*, cirrus in its sac, *r*, seminal vesicle, *s*, sperm duct, formed posteriorly by the union of the two testicular ducts, *t*, the testes, here compact and nearly always double

In the life-history of the Malacocotylea the fertilised egg gives rise to a larva which, in order to complete the cycle, enters another ("intermediate") host; here it usually gives rise asexually to numerous individuals of a second form, and frequently these again to a third form, from which the sexual worm is developed. So that from each egg deposited by the adult a very large number of new flukes are developed.

The adults live in Vertebrata, and nearly always in the enteron or its outgrowths; the intermediate host is usually a mollusc.

FAMILY 1. AMPHISTOMIDAE. Body more or less cylindrical; oral

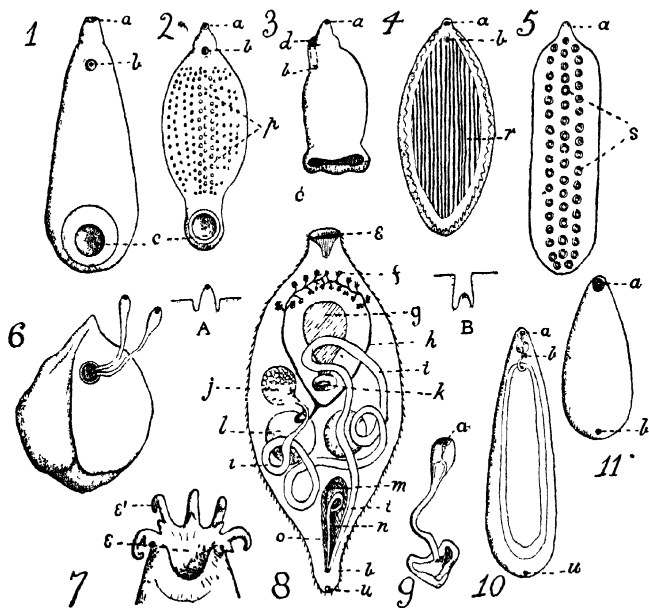


FIG. X —Some Malacocotyleans

Letters common to all the figures, except Fig 8. *a*, mouth and oral sucker, *b*, genital pore, *c*, posterior ventral sucker

1 —*Amphistomum conicum*, Zed, from the paunch of the cow, ventral view (after Laurer). The genital pore is at the apex of a small papilla surrounded by a shallow groove (cf Fig *A*)

2 —*Homologaster paloniae*, Poir, from the caecum of *Palonia* (*Bos*) *frontalis*, ventral view (after Poirier). *p*, the adhesive papillae covering the ventral surface

3 —*Gastrothylax cobboldii*, Poir, from the stomach of *Palonia*, lateral view (after Poirier). The furrow surrounding the genital papilla has become deepened to form a sac (cf Fig. *B*), the entrance to which is labelled *d* Figs *A* and *B* are immediately below 2 and 4 respectively

4 —*Ogmogaster plicata*, Crepl, from the caecum of *Balaenoptera* sp, ventral surface (after Jagerskiold) *r*, the longitudinal ridges constituting a secondary adhesive organ

5 —*Notocotyle serialis*, Dies, from the colon of *Anas penelope*, dorsal surface (after Diesing). *s*, the dorsal suckers in three rows

6 —*Didymozoon thynni*, Tschbg (=*Monostomum bipartitum*, Wedl), from a cyst on the gills of *Thynnus vulgaris* (after Wagener) The two individuals are closely wrapped round one another, their "heads" projecting freely

7 —Anterior sucker of *Gasterostomum fimbriatum*, v Sieb, from the stomach of the pike (after Wagener) *ee'*, the tentacle-like processes from its margin

8 —*Gasterostomum armatum*, Mol., from the intestine of *Cottus scorpio*, ventral view (partly after Molin, partly after Levinsen) *b*, genital pore; *e*, anterior sucker; *f*, vitellarium, *g*, simple sac-like intestine; *h*, the left vitelline duct, which unites with its fellow, and opens by a median duct into the germ duct; *i*, uterus; *j*, germarium, *k*, mouth, which has a position unique amongst the Trematoda, nearly in the middle of the ventral surface; *l*, the right testis; *m*, seminal vesicle; *n*, cirrus sac, *o*, cirrus or penis, *u*, excretory pore

9.—The smaller of the two individuals of *Didymozoon*, probably the male. (After Wagener.)

10.—*Monostomum mutabile*, Zed, from the sub-orbital sinus and body cavity of various aquatic birds. (After P. J van Beneden) *u*, excretory pore

11 —*Opisthotrema cochleare*, Lkt., from the tympanic cavity and Eustachian tube of *Halicore*, ventral view (modified from Fischer). The genital pore (*b*) is posteriorly placed.

sucker small; posterior sucker terminal, usually large, and in front of it fixing papillae may be developed on the ventral surface. *Amphistomum*, Rud. (Fig. X. 1); numerous species in various mammals. *A.* (*Diplodiscus*) *subclavatum*, Goeze, in rectum of Amphibia (see 30). *Gastrothylax*, Poir. (Fig. X. 3); *Homalogaster*, Poir. (Fig. X. 2); *Gastrodiscus*, Cobb.; *G. polymastos*, Leuckt., in colon of horse. *Aspidocotyle*, Dies., intestine of fish (Monticelli places the genus in the order Aspidocotylea). FAMILY 2. DISTOMIDAE. The posterior sucker has shifted forwards along the ventral surface, so as to come to lie in the middle of the body, or even in front of this point; no adhesive papillae, though spines are frequently developed on the surface of the body; the genital pore is almost always in front of the ventral sucker, usually in the middle line, rarely shifting to the side (see 32, 38, and Fig. XI.). *Distomum*, Retzius (= *Fasciola*, L., *in parte*), no retractile boring proboscis; hermaphrodite. The genus has been subdivided into eleven sub-genera. Sg. *Cladocoelium*, Duj.; *D. hepaticum*, L., occurs in the bile ducts of various mammals, especially common in sheep, but also in man, kangaroo, ox, etc. The "Liver-fluke" is so commonly taken as a "type" of the Trematoda, that a brief historical account of it may be of interest.

Being the cause of a disease—"sheep-rot"—in a domesticated animal it naturally claimed the attention of naturalists and others in early times; the first account of an epidemic of this disease being given by Gemma (1575) as having occurred in 1552 in Holland The earlier writers believed the parasite to occur in the blood-vessels of the liver, till Faber (1670) established the fact that it occurs not in the blood-vessels but in the gall bladder and bile ducts and their capillaries (*vermis e ductu cystico et poro biliario*) Ruysch (1691) gives the first (but extremely poor) picture of the "fluke." Redi, who was acquainted with quite a number of parasites of birds, mammals, etc., referred to the fluke as *vermis vervecini hepatis*, and gives a fairly good figure of it.

Faint inklings of its life-history occur in Gesner's work (1551), where he mentions that in France it had been noticed that in the livers of sheep, which had eaten certain plants growing by the water's side, and termed "duva," small leech-like animals were found, causing a disease in the sheep to which the name "duva" was given. These two uses of the word still exist; *douve* in modern French is "spearwort," and *douve de foie* is the liver-fluke. Leeuwenhoek, however, did not connect the fluke with eating, but believed that the flukes live freely in the water and make their way into the gall bladder of the sheep, while the host is drinking.

Romberg (1706), on the other hand, who discovered flukes in the calf, regarded them as *vermes cucurbitini* (a term used at that time for isolated proglottids of Cestodes). Pallas (1760) was the first to add man to the list of hosts.

The correct name of the liver-fluke is even now a matter of discussion amongst purists of nomenclature. Linnaeus (1746) used the word *Fasciola* to include the "fluke," a fish Cestode (*Schistocephalus*), and a Triclad (*Dendrocoelum*), under the belief that they were all stages in one life-history, starting with the Planarian; and to this assemblage gave

the name *F. hepatica ovata.* But Retzius (1776) invented the name *Distoma* for the Trematodes, of which several were then known, retaining *Fasciola* for something quite different (viz. *Gordius*); O. F. Muller (1776) also separated Linné's *Fasciola* into two, retaining the name for a Trematode and giving *Planaria* to the Turbellarian, and for some

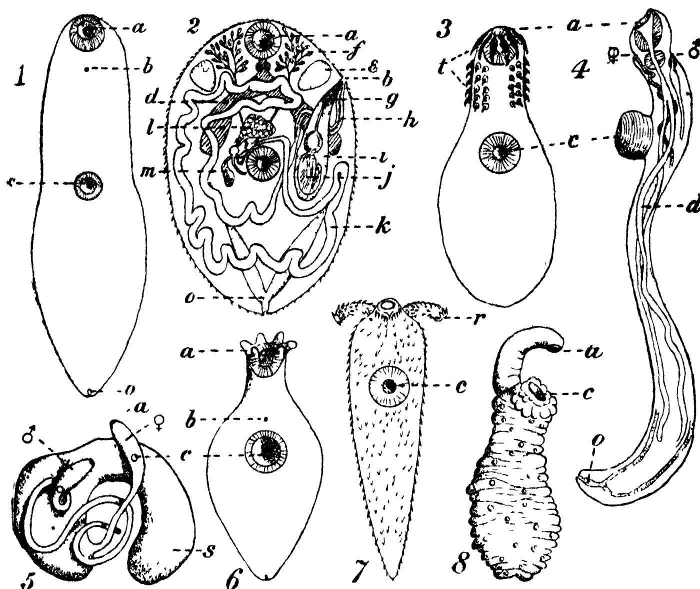


Fig XI —A Group of Distomidae

1 —*Distomum variegatum*, Rud (after Looss), from the lung of *Rana esculenta*, to show the general shape and disposition of the suckers. Its anatomy agrees closely with the generalised "type" (see Fig IX).
2 —*D. confusum*, Looss, from the intestine of frog and toad The genital pore has shifted in this and some other species to the left margin of the animal In this case the other organs have undergone peculiar shiftings from the normal. The testes and vitellaria are anterior (After Looss.)
3 —*D. acanthocephalum*, Stoss (after Stossich), from the rectum of *Belone acus* *t*, hooklets
4.—*D miescheri*, Zsch (after Zschokke), from the oesophagus of *Trutta salar*, side view to illustrate the fact that the male (♂) and female pores (♀) may be separate
5 —*Koellikeria filicolle*, Rud (*D okenii*, Kol), from cysts in the branchial chamber of *Brama raji* (partly after Kolliker)
6 —*D. nodulosum*, Zed (after Looss), from the intestine of *Acerina cernua*, to show tentacles.
7 —*Rhopalophorus horridus*, Dies , from the duodenum of *Didelphys myosurus*, ventral view (after Diesing) *r*, armed tentacles.
8.—*D. verrucosum*, Poir., from stomach of *Thynnus* (after Poirier)
a, mouth and oral sucker; *b*, genital pore, *c*, ventral sucker, *d*, intestine; *f*, vitellaria; *e*, testis; *g*, cirrus, *h*, vaginal region of uterus, *i*, cirrus sac, *j*, seminal vesicle, *k*, uterus, *l*, germarium, *m*, spermatheca, *s*, enlarged sac of ♀ *Koellikeria*, *o*, excretory pore.

time *Fasciola hepatica* was the name of the liver-fluke. Zeder and Rudolphi, however, returned to Retzius's name *Distoma*, which Nitzsch (1816) altered to *Distomum*; and since that time, with a few dissentients, this modification of Retzius's name has been employed.

The anatomy of the liver-fluke may be found in nearly every text-book, and has been the subject of much work by Leuckart in his well-

known work on "Parasites"; while Sommer (40) made a special study of it, the illustrations to which are copied in nearly all accounts. Raillet has recently (1890) proved experimentally that it sucks the blood, and does not feed upon the bile of its host.

Sg. *Dicrocoelium*, Duj.; *D. cylindraceum*, Zed., lung of frog. *D. reflexum*, Crepl., oesophagus of salmon. Sg. *Podocotyle*, Duj., only in the intestine of fishes. Sg. *Brachycoelium*, Duj.; *D. claviformis*, Brds., in rectum of *Tringa alpina*. *D. rubellum*, Olss., intestine of *Labrus*. *D. heteroporum*, Duj., intestine of bats. Sg. *Brachylaimus*, Duj.; *D. tereticolle*, Rud., in pike. *D. variegatum*, Rud, lung of frog (Fig. XI. 1). Sg. *Apoblema*, Duj, in fishes only. *D. appendiculatum*, Rud., in *Clupea alosa*. Sg. *Echinostoma*, Duj.; *D. trigonocephalum*, Rud., intestine of various carnivora; other sp in fishes, birds, and mammals. Sg. *Crossodera*, Duj., in fishes only. *D. nodulosum*, Zed., intestine of perch (Fig. XI. 6). Sg. *Cephalogonimus*, Poir.; *D. lenoiri*, Poir.,

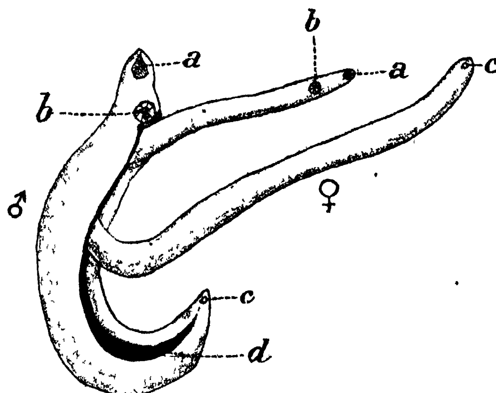


Fig XII.—*Bilharzia haematobia*, v Sieb, from the Blood of Man. (After Fritsch.)

♂, the male, ♀, the female *a*, mouth, *b*, ventral sucker, *c*, excretory pore, *d*, gynaecophoral groove on the ventral surface of the male, in which lies the genital pore, and the sides of which clasp the female

in Chelonian. Sg *Urogonimus*, Montic.; *D. macrostomum*, Rud., in *Fringilla*, etc. Sg. *Mesogonimus*, Montic.; *D. westermanni*, Kerb., in lung of man, dog, cat, tiger; Europe and U.S A.

The genus *Rhopalophorus*, Dies, has two retractile tentacles, armed with hooklets at the anterior end of the body. *R. coronatus*, Rud. (Fig. XI. 7); *Bilharzia*, Cobbold (*Gynaecophorus*, Dies.), the sexes are separate and dimorphic (Fig. XII.); the male is smaller than the female, which he carries in a ventral (gynaecophoral) groove, posterior to the ventral sucker, and in which the genital pore lies; the anterior part of the body is cylindrical, the groove being formed by an inrolling of the sides; they live always in pairs in blood-vessels of mammals, in hot climates (see 33). *B. haematobia*, Bilh., in the abdominal veins of natives of Africa, in some parts of which nearly half the inhabitants are infected. The eggs are laid in the blood, accumulate in the capillaries, and cause inflammation and rupture of the vessels. According to Sonsino,

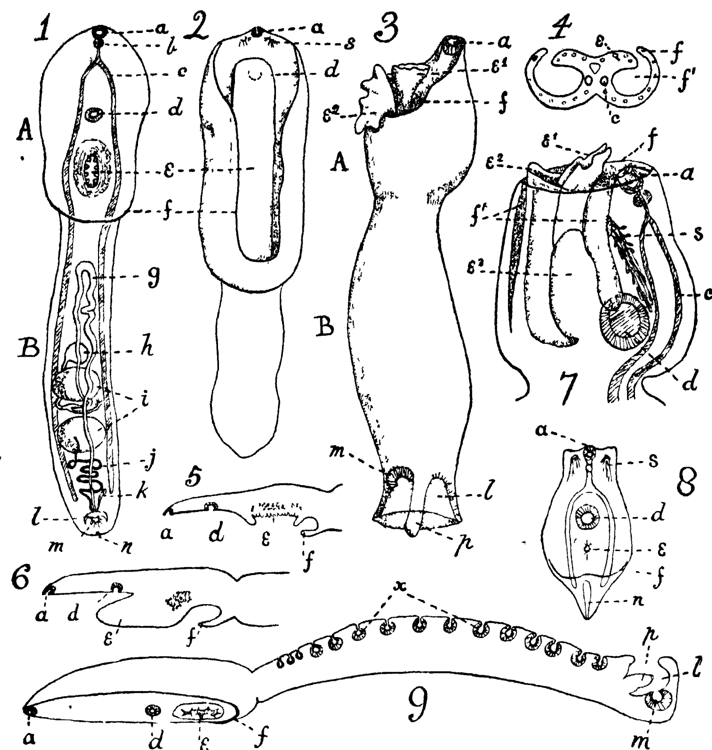


FIG XIII —A Group of Holostomidae

1.—*Diplostomum longum*, Brds, from intestine of Brazilian crocodile (after Brandes), ventral view The anterior region of the body (*A*) is well marked off from the tail-like genital region (*B*), which is cylindrical The latero-posterior margin (*f*) of *A* is slightly prominent. The new adhesive organ (*e*) consists of a pit, from the bottom rise glandular papillae (cf Fig 5)

2 —*Hemistomum clathratum*, Dies, from intestine of *Lutra brasiliensis* (after Brandes) The margin (*f*) of the fore body is curved inwards and partially conceals the accessory adhesive organ (*e*), which has the form of a long ridge (cf. Figs 4 and 6), the edge of which overhangs the base and hides the ventral sucker (*d*)

3 —*Holost variabile*, Nitzsch (modified from Molin and Brandes), from intestine of various carnivorous birds The margin (*f*) of the fore body has now bent round and fused to form a cup from which the elaborate "accessory organ" projects At the posterior end is seen the "bursa copulatrix" (*l*)—characteristic of the family—with the genital sucker (*m*) and papilla (*p*) carrying the genital pore

4 —Transverse section of *Hemistomum*. *c*, intestine, the numerous small circles are sections of the excretory canals which invade the organ

5 —Longitudinal section of the fore body of *Diplostomum*, Brds, to show the prominent hinder margin (*f*)

6 —*Hemistomum* Longitudinal section of the fore body to show the foot-like accessory organ *e*

7 —*Holostomum* (after Brandes) Diagrammatic transparent view of the fore body

8.—"Tetracotyle" (partly original)

9.—Side view of *Polycotyle ornata*, Wilh -Suhm, from the gut of *Alligator lucius* (partly diagrammatic, after Poirier) *x*, the several dorsal suckers of hind body

Letters common to all figures · *A*, fore body, *B*, hind body or genital region *a*, mouth and buccal sucker, *b*, pharynx, *c*, intestine; *d*, ventral sucker, *e*, accessory adhesive apparatus, e^1, e^2, its parts in *Holostomum*, *f*, the prominent and incurved margin of the fore body, *f'*, the cup produced; *g*, uterus, *h*, germarium; *i*, testis; *j*, sperm duct, *k*, prostate; *l*, bursa copulatrix; *m*, genital (copulatory) sucker, *n*, excretory pore and bladder; *p*, genital papilla; *s*, glands in connection with accessory apparatus.

the intermediate host is a small crustacean, into which *Bilharzia* penetrates and encysts; the host is swallowed, with the water, by man. *B. magna*, Cobb., in the vena cava of *Cercopithecus fuliginosus*. *B. bovis*, Sons., in domestic cow; Egypt and Sicily. *Koellikeria*, Cobb., unisexual, dimorphic; the male thread-like, the female swollen posteriorly (Fig. XI. 5); they live coiled together in pairs, encysted in the oral and branchial cavity of marine fish. FAMILY 3. HOLOSTOMIDAE. The body is divided into two regions: in the hinder, cylindrical, tail-like region the genital organs are developed, the copulatory aperture of which is at the posterior end, where a sucker is developed. In addition to the normal two suckers, which are both situated in the anterior region of the body, there is developed here an adhesive apparatus by the inrolling of the sides to a greater or less extent The members of this family present no "asexual" generation in their life history; each egg gives rise to only one sexual worm, but passes through a larval stage, which, when encysted in an intermediate host, is known as "Tetracotyle," and resembles a cercaria;[1] for an account of anatomy and development, see 10, 12). *Diplostomum*, v. Nordm, in birds and crocodiles (Fig. XIII). *Hemistomum*, Dies., numerous species in birds and mammals (Fig XIII. 2). *H. excavatum*, Nit, in *Ciconia alba*, has a larva living in *Rana temporaria*. *Holostomum*, Nit., numerous species in intestine of birds, *H. variegatum*, in *Larus ridibundus* and other birds, has as larva *Tetracotyle ovata*, v. Linstow, which occurs encysted in the peritoneum, in the head and elsewhere of *Acerina cornua* *H. variabile*, Nitzsch (Fig. XIII. 3), has as larva, *Tetracotyle colubri*, v Linst Ercolani was the first to prove by feeding experiments that "Tetracotyle" or "Diplostomum" develops into *Holostomum*. *Polycotyle*, W Suhm.; *P. ornata*, W. S, gut of *Alligator lucius*. FAMILY 4 MONOSTOMIDAE The characteristic posterior sucker has disappeared, but the oral sucker (everted pharynx according to Monticelli) remains The genital pore usually occupies the normal position; there is no Laurer's canal *Monostomum*, Zed. (Fig X. 10); many species in all vertebrates (see 47). *Opisthotrema*, Lkt. (Fig X. 11); *Notocotyle*, Dies., in birds (Fig. X. 5). *Ogmogaster*, Jaeg, in Cetacea (Fig. X. 4). FAMILY 5. GASTEROSTOMIDAE. Mouth ventral; anterior terminal sucker imperforate, surrounded by tentacular-like processes; genital pore at the hinder end of body; intestine sac-like, unforked, short. *Gasterostomum*, v. Sieb., in intestine of fish (Fig. X. 8). *Gasterostomum fimbriatum*, v. Sieb., lives in *Perca fluviatilis*; the egg gives rise to a larva which makes its way into *Unio* or *Anodon*; a sporocyst is formed in the liver or gonad; and within this arises the peculiar cercaria known as *Bucephalus*, v Baer (1), from its resemblance to the head of an ox (Fig. XIV). When liberated they make their way out through the exhalant siphon and live freely in the water for a few hours. This cercaria is destined to be swallowed by the second intermediate host, *Leuciscus erythrophthalmus*, in which it encysts itself in the wall of the mouth, or on the gills, and when *Leuciscus* is devoured by the perch, the cyst is dissolved, and sets free *Gasterostomum*, into which *Bucephalus* (as Wagener showed,

[1] In specimens of *Ammocoetes* great numbers of Tetracotyle sometimes occur in the vascular membrane covering the brain (Brown, *Qu. J. Mic. Sc.* xli. p. 489, 1899).

1858) has meanwhile changed. *Gasterostomum*, sp. of the shark, has as first intermediate host *Ostrea*, *Cardium*, etc., whence issues *Buceph. haimeanus*, which makes its way into a second host, the fish *Belone*. The sporocysts castrate the mollusc which they attack. FAMILY 6. DIDYMOZOONIDAE, Montic., live in pairs, encysted on the surface, oral cavity, or branchial chamber of fishes; the anterior sucker alone is present; the genital pore is in front of the oral sucker. *Didymozoon*, Taschb. (Fig. X. 6, 9); *Nematobothrium*, v. Ben.

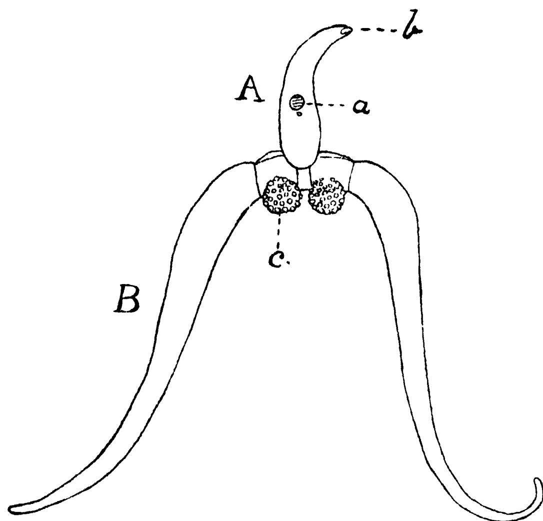


FIG XIV

Bucephalus polymorphus, v Baer The forked-tailed cercaria of *Gasterostomum fimbriatum*, v Sieb The cercaria occurs in *Anodon*, etc., the adult in *Leuciscus*, sp *A*, the body, *B*, the bifurcate tail, *a*, the pharynx, behind which is the mouth, in the centre of the body, *b*, the pear-shaped glandular organ, which is replaced by the anterior sucker during its metamorphosis, *c*, the *ansatzstuck* at the base of each limb of the bifurcate tail, between them is seen the base or median portion of the tail

Further Remarks on the Order Malacocotylea.—Whereas the general statement is true that sexual forms of this group occur only in Vertebrata, there are at least two species of *Distomum* which constitute exceptions:—

D. echiuri, Greef, is found in the nephridium of the male gephyrean *Echiurus pallasii*. *D. rhizophysae*, Stud., occurs in the siphonophorous hydrozoan, *Rhizophysa conifera*. An encysted Distoma has been found in the tentacles of Synapta, and the viscera of Ophiurids, by Cuénot (1892).

Further, several sexless, not encysted, cercariae have been recorded from various marine non-molluscan animals: *D. pelagiae*, Köll., in the gonads of *Pelagia*; *D. hippopodii*, C. Vogt; *D. cesti-*

veneris, Vogt; and others, from body cavity of *Sagitta*, *Salpa*, *Velella*, etc.

In addition to a number of anatomical peculiarities in the

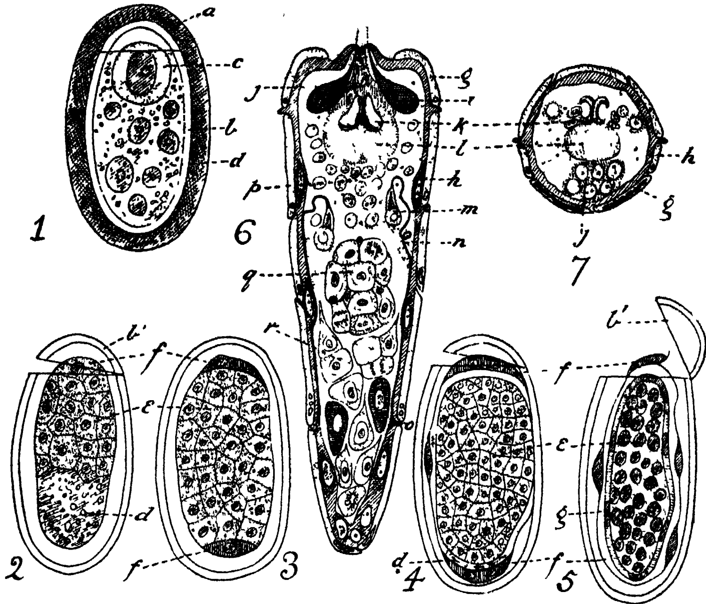


FIG XV —Development of Embryo of *Distomum tereticolle*. (From Schauinsland)

1.—The living egg with its gelatinous envelope (*a*), *b*, egg shell deposited in ootype; *c*, germ cell with large nucleus, *d*, vitelline cells, outlines not distinguishable in living egg, but the seven nuclei indicate the number of cells

2 —Segmentation of the germ cell has resulted in a solid blastosphere, the yolk is greatly reduced One of the blastomeres (*f*) at the upper pore is larger than the rest

3 —This cap cell has divided and given rise to three cells, two at one pole, one at the other The yolk is nearly absorbed and is not represented in this figure

4.—The cap cells have flattened out and form a "yolk envelope," investing the embryo and the remains of the yolk, two nuclei are seen above, two below, and one on the left side

5.—The embryo, after separation of the yolk envelope, has become differentiated into an outer layer of flat cells or ectoderm (*g*) and a central mass (*e*), four nuclei of the shell membrane are seen, *b'*, operculum

6 —Longitudinal section of the larva or miracidium of *Distomum hepaticum* (From Coe in *Zool Jahrb* ix 1896 (Anat), p 561) *g*, flat epidermal ciliated cells, derived from *g* in Fig. 5, *h*, the underlying cellular cutis, *i*, head glands (Coe), one on each side of the body, each with a narrow duct opening on the tip of the head papilla, which is represented partially retracted, the secretion is indicated by a row of dots, *j*, the vestigial enteron, *k*, eyes, resting upon the brain (*l*), *m*, flame cell, on each side, whence a fine duct (*n*) passes backwards to open to the exterior at (*o*) excretory pore, *p*, general parenchyma, *q*, a germ ball, *r*, germ cells, posteriorly, lying in a cavity which appears to represent the coelom

7 —Transverse section of the embryo at the level of the eyes *g*, ectoderm cell, with its peculiar elongated filamentous nucleus cut longitudinally. In Fig 6 the nuclei are cut transversely, and appear in the hind end of each cell Other letters as before. The nuclei outside the eye are possibly part of a sensory apparatus. Coe was unable to see the retractor muscles of Leuckart.

nervous and reproductive system, to which reference is made below, the most striking and interesting differences between the Heterocotylea and the Malacocotylea lie in the developmental history, to illustrate which a concrete example may be described.

The early stages of development up to the formation of a free-swimming larva are best known for *Dist. tereticolle*, from the pike (Schauinsland, 39). The egg cell is embedded near the anterior end of the egg in a mass of yolk cells; segmentation is total, and nearly regular, giving rise to a solid blastosphere (Fig. XV.). At the anterior pole one cell delays in its further segmentation, whilst the rest continue to divide and give rise to smaller cells; this apical anterior cell flattens out and divides into two; these (after further subdivision) spread over the yolk cells, which have in the meantime diminished in size and undergone a certain amount of disintegration. Other flat cells make their appearance posteriorly, and extend forwards; in this way a "yolk envelope" of flat cells is formed which lies immediately within the egg shell, and is left behind within it when the larva escapes. This envelopment of yolk by blastomeres is similar to what happens in Triclads. Meanwhile, the other blastomeres have become differentiated into a flat epiblast, which becomes ciliated, and a central mass of cells in which, later, the enteron becomes marked out (? by delamination) as a simple sac.

Between the enteron and the epiblast there is developed from the central mass two layers of muscles, which are in many cases separated from the gut by a distinct cavity, which is lined by a layer of cells and may be regarded as coelom. The coelom may, however, in other cases be more or less blocked up by cells of an embryonic character, probably derived directly from blastomeres.

The egg, having passed out of the host's body with the faeces, undergoes its development in the water. The young larva, or "miracidium" (M Braun), or "ciliated embryo" (*auctorum*), now leaves the egg, and the further history has been most fully studied in the case of *D. hepaticum* (by Leuckart, 27; and Thomas, 43), and in *D. cygnoides* (by Wagener, 45). The eggs of these flukes pass out of the host with the faeces, as King was the first to show for the liver-fluke (1836); and the miracidium escapes into the water. It is to all intents and purposes a Rhabdocoelous Turbellarian without gonads; its shape and structure are shown in Fig. XV. 6, 7, and Fig. XVI. 1.

At the apex of the snout, which is moved by muscles, is situated the mouth—armed with a stylet in the case of *D. lanceolatum* and others—which leads into the short, sac-like enteron. Locomotion is effected by the ciliated epiblast, aided by the somatic muscles. Cilia are generally regularly developed all over the surface, or in some species limited to definite areas, but are never in bands; a pair of eyes—recalling in their structure those of adult Heterocotyleans—rests upon the brain; a pair of flame cells represents the excretory system, and are said to be derived from the epiblast (Fig. XV. 6, *m*).

The miracidium (Fig. XVI.), once set free, swims about seeking for a definite mollusc, into which it will bore its way by means of the snout. Wagener (1857) was the first to observe the

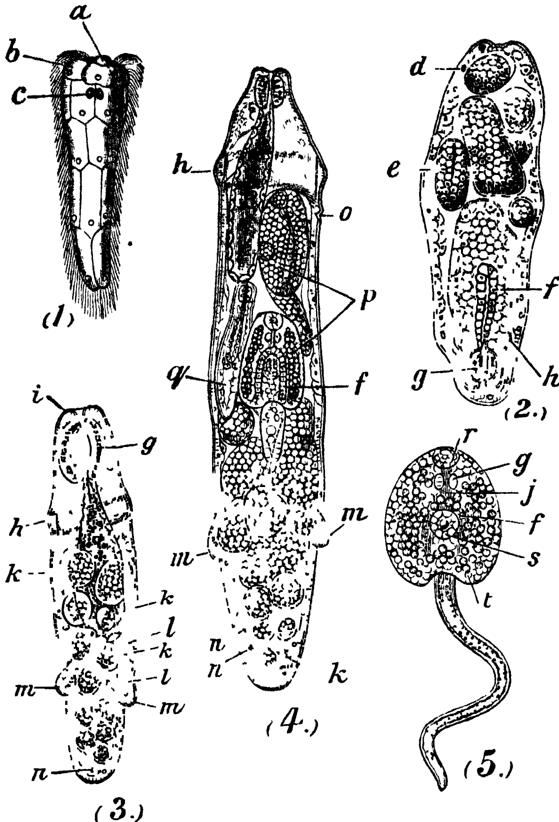


FIG. XVI.—The life-history of *Distomum hepaticum*. (After Thomas.)

1.—The free swimming larva, or "miracidium," showing external appearance
2.—Sporocyst, containing germ balls and young rediae
3.—A young redia, containing germ balls; the enteron is shaded but unlettered
4.—A fully formed redia, containing a daughter redia, two cercariae, and germ balls.
5.—A free cercaria

a, head papilla; *b*, anterior ring of ectoderm cells; *c*, eyes; *d*, same, degenerating, in sporocyst; *e*, embryo, at gastrula phase, in sporocyst; *f*, enteron of young redia; *g*, pharynx; *h*, collar of redia; *i*, lip; *j*, oesophagus of cercaria; *k*, "germs," at blastosphere stage; *l*, parenchyma; *m*, posterior, locomotive processes of redia; *n*, germ cells, in wall of redia; *o*, birth opening; *p*, young cercariae in redia; *q*, daughter redia in redia; *r*, circumoral sucker of cercaria; *s*, ventral sucker; *t*, cystogenous cells

entrance into a mollusc in the case of *D. cygnoides*. In the case of *D. hepaticum* this "intermediate host" is *Limnaeus truncatulus*, as was proved by Thomas (42). The animal makes its way into the liver, and undergoes a degeneration—a result no doubt of its

parasitism; it loses its cilia and the cells that bear them. The enteron, meanwhile, undergoes obliteration and degeneration.[1]

The organism is now known as a "sporocyst" (Filippi), and the "germ cells" which occupy the cavity begin to divide up to form "egg-balls" (Fig. XVI. 2). According to some authorities, the "germ cells" are directly derived from undifferentiated blastomeres (Leuckart, Schauinsland), whilst others have described them as arising by division from the cells of the body wall (Thomas, Biehringer, 7; Heckert, 20).

Anyhow, the germ balls consist of cells of different sizes, and soon a flat epithelium is differentiated around a central mass, the epithelial cells are said to lose their nuclei and become cuticularised (Leuckart), while from the central mass a new outer layer becomes differentiated, and thereafter the history is very similar to that by which the miracidium was produced. By a series of changes there is developed from each germ ball another larval form, which is known as "Redia" (Filippi), or "king's yellow worm" (Bojanus and Swammerdam were the first to observe this stage, 1737); within this a new generation of "germ balls" is already formed (Fig. XVI. 2, 3).

The redia differs from the miracidium, in the absence of cilia and of eyes, in the possession of a pharynx, and in the general shape. The rediae escape from the sporocyst, the aperture closes, and the wound heals. The rediae in their turn produce a new generation, the "Cercaria" (O. F. Muller), in the same way, no doubt, as they themselves were produced. But one or more new generations of rediae may be produced by rediae ere the cercariae are formed.

The cercariae, several of which are produced in a redia, escape one by one through a definite birth-pore (as was first noted by Bojanus). The cercaria possesses all the organs of the young fluke in a rudimentary condition, even the foundations of the genital organs are present; in addition, there are the tail, cystogenous glands, and, in some cases, eyes, stylets, and rod cells, organs only used during the brief larval life (Fig. XVI. 5).

This third generation now leaves the snail, swims freely in the water by the movement of its tail, and having attached itself to a blade of grass by means of its ventral sucker, secretes a "mucous" substance around itself which soon hardens to form a cyst (this fact was known to Nitzsch, 1807). This cyst is devoured with the grass by a sheep, the final host of *D. hepaticum*, the cyst is dissolved in the host's stomach, and the tail having in the meantime dropped off or undergone degeneration, a young fluke emerges, and makes its way up the bile duct and into its finer branches, where it grows into an adult fluke.

[1] It appears that in Victoria the intermediate host of *D. hepaticum* is *Bulimus tenuistriatus*, according to T. Cherry, *Proc. Roy. Soc. Vict.* viii. (n. s.), 1896, p. 183.

This history is the best known, and is true only within certain limits for the whole group; for in some cases one generation—the redia—is omitted; in other cases the sporocyst may form by gemmation a second generation of sporocysts, within which the cercariae arise.

The sporocyst and redia are always parasitic in some mollusc; but the free-swimming cercaria chooses a great variety of hosts—in fact, nearly any invertebrate may serve, though it is not necessary for it to become parasitic at all; the adult, however, is found in members of all classes of Vertebrata, rarely in Carnivora, and nearly absent in Pigeons and certain other birds; Trematodes are especially common in fishes, aquatic birds, reptiles, insectivorous birds and mammals, and marine mammals.

The cercariae are not all tailed, and this tail may present great differences in size and structure. Many cercariae are known, some parasitic, others free-swimming, whose adult stage is unknown. And, as in the case of the adult fluke, a species of cercaria may enter a variety of species of host; thus *C. armata* enters *Paludina* and *Planorbis*, further, one host may contain quite a number of different species of cercaria, *e.g.* *L. stagnalis*, may harbour as many as eight species. Cercariae, with a well-developed tail, are most numerous; the tail may be provided with a fin-like membrane (*C. lophocerca*), or with bunches of "setae," regularly arranged (*C. setifera*), (Fig. XVII.). It acquires an enormous development in *C macrocerca* from *Cyclas*, and in *C. elegans*, which occurs free in the sea. The tail is retractile in *C. mirabilis;* it is bifurcated in *Bucephalus.* The tail is quite rudimentary in *C. limacis* and others, while the tail is absent ("cercariaea") in *Leucochloridium* and others which live in terrestrial molluscs

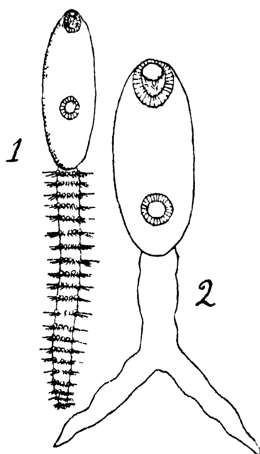


Fig XVII.

1.—*Cercaria setifera*, Villot, in a state of extension, the long tail is provided with a series of circles of stiff bristles.
2 —*C fissicauda*, Villot Both occur in the marine lamellibranch *Scrobicularia tenuis.* (After Villot.)

There is thus produced in the life-history of the Malacocotylea a considerable number of flukes from each egg cell by the intervention at one or more stages of some form of non-sexual reproduction; these asexual forms live in a host different from that of the sexual fluke; hence van Beneden gave the name *Digenea* to the group. But amongst the Digenea were included *Aspidogaster* and the Holostomidae, which do not agree with this general history. *Aspidogaster* has, owing to the possession of a number of anatomical peculiarities, been removed from the group. The Holostomidae

present this difference from the rest of the Malacocotylea; the *young form, after entering the intermediate host, does not reproduce* asexually, but *develops by a metamorphosis into the adult form,* when the intermediate host is swallowed by the final host; Leuckart has used the term "metastatic" in reference to this life-history.

This life-history of the common fluke is a favourite example of "alternation of generations," or metagenesis, on the view that the mode of reproduction in sporocyst and redia is an asexual one (viz. budding); but Grobben first suggested that the cells which give rise to "germ balls" are essentially ova, and that it is a case of parthenogenesis—a view with which Leuckart essentially agrees. In that case, the process is one of "heterogamy" (Leuckart); but this term is more generally applied to cases in which two sexual methods alternate, as in *Rhabdonema nigrovenosum;* and Schwarze has invented the term "alloiogenesis" to indicate alternation of parthenogenesis with sexual reproduction. Claus, regarding the redia and sporocyst as larvae, sees in the history an example of heterogamy with paedogenesis.

Leuckart, Balfour, and Looss regard the whole process as one of a metamorphosis distributed over two or more stages (or generations), as a result of the appearance of vertebrates on earth, for before their appearance the flukes must have attained maturity in an invertebrate, which, on the evolution of vertebrates, became the intermediate host. Looss (30) has further shown that the sporocyst, redia, and cercaria are all built upon a common plan, and represent successive stages in development, the last being entirely fluke-like, except for the full development of the generative organs.

The life-history of *D. macrostomum* is of interest in that the redia and the free-living stage of the miracidium and cercaria are omitted (see 20). The fluke inhabits the intestine of various singing birds, and its eggs pass out with the faeces of its host, which, falling on a leaf, may with it be eaten by the gastropod *Succinea putris* (Fig XVIII.). In the stomach of the snail the miracidium, of peculiar form, is hatched out, and makes its way through the wall of the intestine into the connective tissue. Here it becomes a sporocyst; this grows very rapidly, absorbing the blood of the host, and gives rise to numerous branches, one or two of which outrun the rest, and push their way into the snail's tentacles. The branches become banded with olive-green or brown, and the structure is now known as *Leucochloridium paradoxum* (discovered by Carus, 1835). Owing to its colouring and pulsations within the tentacle, it is mistaken by birds for a dipterous larva, and is devoured. The "cercariaea," which have in the meantime developed from the germ balls inside the sporocyst, are without tails, which are evidently not required, as the organism never leads an independent free life; they develop in the bird into a fluke.

In *D. ovocaudatum*, from the oral cavity of *Rana esculenta*, the miracidium is deprived of cilia, for the eggs are eaten by the intermediate host (*Planorbis*).

Amphistomum subclavatum lives in the intestine of frog, etc.; the miracidium enters species of *Planorbis*; the cercaria leaves this first host, swims about for a few hours, falls to the bottom and encysts. This happens throughout the summer; and the cysts

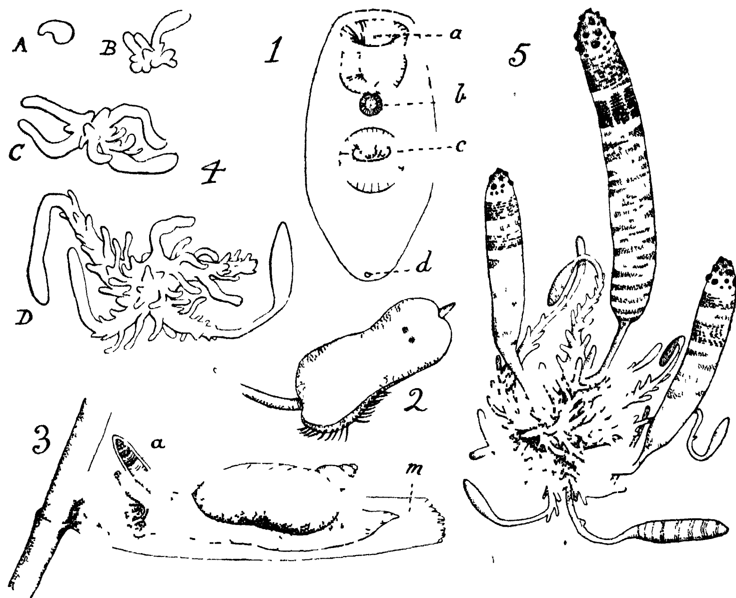


FIG XVIII —The Life-history of *D macrostomum*, Rud (After Heckert.)

1 —Outline of the adult fluke, parasitic in song-birds *a*, mouth surrounded by the oral sucker, *b*, pharynx, *c*, ventral sucker, *d*, genital pore

2 —The miracidium which is hatched in the stomach of the snail

3 —The intermediate host, *Succinea amphibia*, crawling on a leaf (*m*), (nat size) *a*, the cavity of the right tentacle is occupied by *Leucochloridium*. In some cases both tentacles will be similarly occupied

4 —The sporocyst, in various stages of growth, giving rise to a much-branched tube (*D*), the ends of some of the branches becoming enlarged

5 —A fully-grown *Leucochloridium paradoxum*—the elaborate sporocyst which occupies the body cavity of the snail One terminal branch is fully developed, two others are nearly so, and are banded with greens and browns

are devoured by insect larvae, which in their turn are eaten by the final host, the frog, during winter (Looss, 30). Or, according to Lang, the encystment occurs on the skin of frogs and newts, and the cysts are swallowed with the skin when moulting occurs. In this way a gradual passage is formed between cases with and without a second intermediate host.

Further Remarks upon the Class Trematoda.—The animals included in this class are characteristically parasitic, and the two orders,

Heterocotylea and Malacocotylea, exhibit two stages in this parasitism. The former order are nearly exclusively ectoparasitic on marine and fresh-water fish, attaching themselves to the outer surface of the body, or to the wall of the branchial chamber, or to the gills by means of the adhesive apparatus at the posterior end of the body. Less frequently the worms make their way into the canals or tubes formed by the invagination of the epiblast —that is, into the nasal sacs, the oral cavity, and even into the cloaca. The genus *Polystomum* is, as an exception, endoparasitic, living in the urinary bladder of fish, amphibia, or reptiles.

On the other hand, the members of the Malacocotylea, as well as the Aspidocotylea, are essentially endoparasitic, and must be regarded as having passed through an ectoparasitic stage; and, indeed, a few species of *Distomum* still retain this habit. These digenetic Trematodes occur in the enteron and its outgrowths of all groups of vertebrates; the majority live, in the adult condition, in warm-blooded members of the group, many in reptiles and amphibia, and but few (*Distomum* sp.) in fishes. Every system of organ, with the exception of the nervous system and skeleton, is invaded by them, either in a free or encysted condition; and even the blood-vessels are affected by *Bilharzia*.

Although, as in other parasitic animals, it is a general rule that each species attacks only one definite host, as the animal on which the parasite lives is termed, or in hosts nearly related to one another, yet there are instances, such as *Distomum hepaticum* and *D. lanceolatum*, of the same species occurring in many widely different hosts, such as man, rabbit, various ungulates, and even the kangaroo. As in other groups, these parasites are only injurious to the host, when they occur in large numbers, or in certain delicate organs.[1] It is well known that *D. hepaticum*, the liver-fluke, produces "sheep-rot," especially in districts liable to flooding, where the life-history can be readily completed.

The food of Trematodes consists in some cases of slime secreted by the host; and this secretion is, no doubt, increased by the irritation caused by the insertion of hooklets into the host's skin. But more usually nutriment is derived from the blood of the host, which is sucked up by the parasite by means of the powerful pharynx, the intestine is consequently, in the fresh worm, yellowish or red in colour; and remains of blood corpuscles, lymph cells, and epithelial cells have been noted in its contents.

In *Polystomum* peculiar crystals, reddish in colour, and octahedral in form, suggest a derivative of haemoglobin (Zeller).

Some authorities (Taschenberg) describe intracellular digestion, yet there is no doubt but that cavitary digestion also occurs.

[1] It has, however, recently been shown to be extremely probable that Nematodes, Cestodes, and Trematodes excrete an active poison.

The mouth was probably at first employed as a sucker for adhesion to the host during the action of the pharynx, as it now is in *Monocotyle;* the next stage is exhibited by *Onchocotyle*, in which special muscle fibres are developed around the mouth, so as to form an indistinct "oral sucker," which has become much further differentiated in the Malacocotylea. From this condition the arrangement more usually met with in the Heterocotylea may be derived where a pair of suckers are developed, one on each side of the mouth, and communicating with the buccal cavity; these are known as "buccal suckers," and are met with in the majority of the Polystomidae. By the removal of these from the mouth, they lose the connection with the buccal cavity, and a pair of independent "lateral suckers" are formed, as in *Tristomum*.

The posterior adhesive apparatus presents considerable variety. No doubt the single sucker at the hinder end of the body represents the primitive arrangement; this sucker, which is always "simple," and never armed in the Malacocotylea, is usually "multiloculate" in the Aspidocotylea and Heterocotylea, owing to the special development of muscular ridges, giving rise in the former order to transverse and longitudinal, and in the latter to radial ridges, starting from a circular ridge surrounding the centre of the sucker.

It seems not improbable that the six or eight suckers of the Polystomidae, arranged upon a caudal disc or "cotylophore," have been derived phylogenetically by a further development of this arrangement of muscle groups, till the loculi became entirely independent. Finally, in the Microcotylidae, the presumed subdivision of the sucker has gone very much further, resulting in a considerable number of small suckerlets arranged on a membranous cotylophore at the posterior lateral margins of the body; this apparatus must have been derived from the single sucker by the cotylophore extending along each side, instead of remaining terminal.

In the Malacocotylea the primitively posterior sucker has moved forwards in the Distomidae, so as to lie quite far forwards in the ventral surface. But accessory adhesive organs are developed to a greater degree, and in more varied form, in the Malacocotylea than in the Heterocotylea. The papillae covering the ventral surface of *Homalogaster* (Fig. X.) and *Gastrodiscus* are provided with retractile tips, and aid in fixation; they appear, indeed, to be replacing functionally the posterior sucker, which is small in the former, and quite minute in the latter genus. In the Monostomidae this posterior sucker has disappeared, and fixation is effected partly by the oral sucker, but chiefly by the retractile warts along the dorsal or ventral surface of the body (Fig. X.). An accessory organ of quite another type is developed in the Holostomidae, the sides of the fore body being folded over ventrally in various

degrees, so that ultimately the original form of the body is lost (Fig. XIII.).

The posterior sucker or the cotylophore in the Heterocotylea is frequently armed with hooklets or spines, aiding the worm in fixation to its host; whereas hooklets are never present in this organ in the Malacocotylea, or in Aspidocotylea, a fact which struck both Burmeister and Monticelli. Moreover, in the Polystomidae the suckers are strengthened by a special development of the cuticle to form a "chitinoid" skeleton (the substance is soluble in 35 per cent KHO, according to Cerfontaine), (Fig. XIX. 5). In some forms the sucker, when in use, retains its cup shape, when it may be termed "acetabulate," or it becomes folded across its middle, like the two valves of a lamellibranch shell, holding on to the host like a pair of forceps, when it may be termed "valvate" (Fig. XIX. 4).

The muscles which constitute the sucker present some variety in their arrangement (Goto). For instance, in *Calicotyle*, three sets of muscles are distinguishable: (*a*) radial along the ridges, derived from the longitudinal muscles of the body; (*b*) circular muscles round the margin; (*c*) dorso-ventral fibres traversing the substance of the sucker from the dorsal body wall (Fig. XIX. 3).

On the other hand, the wall of the suckers in Polystomidae consists of muscular fibres, arranged at right angles to the surface, in between the chitinoid skeleton, and limited, bodywards, by a distinct membrane, these may be considered " intrinsic"; while muscle fibres from the general somatic musculature are attached to the skeleton, and on their contraction the floor of the apparatus is raised, and the sucking action produced (Fig. XIX. 6). In valvate suckers other muscle fibres are attached to the various pieces of the skeleton, serving as occlusor, divaricator, and constrictor muscles.

It is an interesting fact that in *Monocotyle* (Goto) and in *Diclidophora* (Cerfontaine) the intrinsic muscles are transversely striated.

Apart from the existence of an elaborate adhesive apparatus, which is foreshadowed by the sucker of some Polyclads and Triclads, the Trematodes differ from the Turbellaria in only one essential particular, and that is in the nature of the outer covering of the body; for with the parasitic habit the cilia of the ancestral Platyhelminth have gone, and the whole body is covered by a thick, firm "cuticle," or "investing membrane" (Wright). There can be little doubt but that this cuticle which occurs also in Cestoidea and Nematoidea has been developed in relation to the parasitic life, and serves as an efficient protection against the action of digestive or other secretions of the host. In the Heterocotylea and Aspidocotylea this cuticle is comparatively simple; in the Malacocotylea it is frequently armed with minute

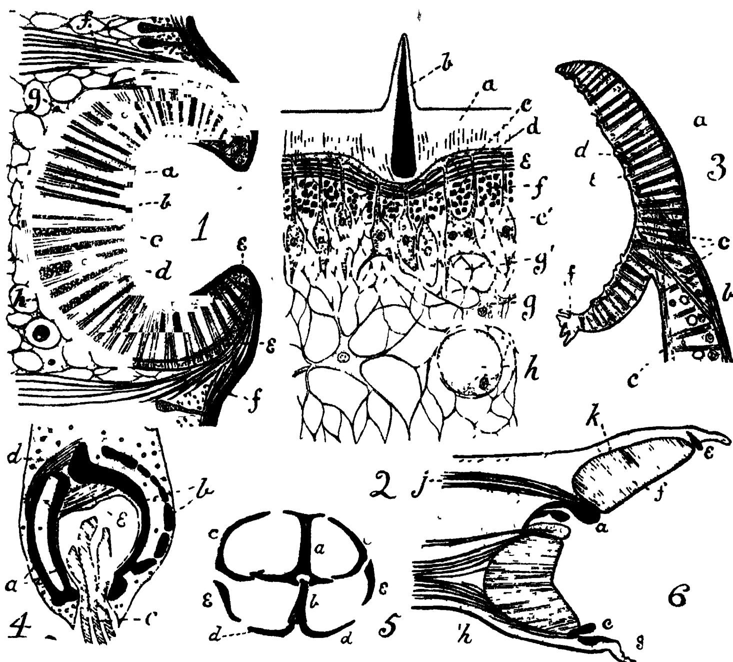


Fig XIX

1 —Transverse section of the ventral sucker and neighbouring part of the body of *Distomum hepaticum* (orig) *a*, cuticle, *b*, outer transverse muscles, which appear to become continuous around the margin with the inner transverse muscle (*h*), *c*, radial muscles passing through the whole depth of the sucker, the bundles of muscle fibres are separated by connective tissue represented by dots, in which the large myoblasts (*d*) are embedded, two of which are shown in the section, *ee*, circular muscle fibres, chiefly developed around the margin of the sucker, *f*, retractor muscles of the sucker, derived from the dorso-ventral body muscles, which serve to move the sucker as a whole, *g*, the internal limiting cuticular sheath of the sucker, *h*, the internal transverse muscles of the sucker

2 —Diagrammatic transverse section through the body wall of a Trematode, composed from descriptions and figures of various authors, and from my own observations *a*, the cuticle, vertically striped in its deeper portions, *b*, spinelet, occurring in Malacocotylea, *c*, subcuticular protoplasmic layer joining the upper ends of the epidermal cells (*c'*), which have been separated from one another by the upgrowth of the mesoblastic tissues Below this layer is the basement membrane (*d*), *e*, circular layer of muscles, *f*, longitudinal layer of muscles, *g*, branched parenchymal cell, the processes of which subdivide and anastomose to form a network (*g'*) of fine threads invading the muscular and epidermal layers, *h*, a "vesicular cell," such as occurs in various Trematodes, in greater or less abundance

3 —Longitudinal section through the posterior sucker and the hinder end of the body of *Tristomum ovale* (from Goto) *a*, sucker, not delimited internally from the tissues of the body (*b*), *c*, longitudinal muscles of the body passing into the sucker and spreading out therein, *d*, radial or dorso-ventral muscles, between the bundles are groups of "sticking glands" not indicated, *e*, transverse muscles, *f*, marginal membrane

4 —Longitudinal section through one of the eight suckers of *Dactylocotyle denticulatum*, Olss (from Cerfontaine), which is parasitic on the gill filaments of *Gadus carbonarius* The sucker is "valvate" and armed, the figure shows the armature, but not the muscular sucker, and three branchial filaments are clasped *a*, *b*, chitinoid armature, *c*, gill filaments, *d*, divaricator muscles, serving to open the valves, *e*, occlusor muscles

5 —The chitinoid skeleton (armature) of a sucker of *Diclidophora elongata*, the skeleton consists of three pairs of pieces (*cde*) set round the margin of the sucker, and two transverse unpaired pieces (*ab*)

6 —Longitudinal section through one of the eight suckers of *Cycl sessilis*, Goto, from the oral cavity of *Chaerops japonicus*. The sucker is limited internally (*k*), but the intrinsic muscles are subdivided by the skeleton, *ace* (cf Fig 5), to which, as well as to the sucker itself, retractor and other muscles (*hj*) are inserted for its movement, *g*, the marginal membrane.

spines scattered over the entire surface of the body (Fig. XIX. 2), or carried, in *Rhopalophorus*, on two great tentacle-like processes of the anterior end of the body (Fig. XI. 7), while in *Echinostoma* the oral sucker is armed with spines (Fig. XI. 3). These spines may be compared with those of *Enantia*, amongst Turbellaria, and, like the cuticle, appear to be chitinous; they aid in attachment, and perhaps in obtaining blood. The cuticle presents two or three layers, differing in optical characters; there are no pore canals. Below the cuticle is a slight, granular "subcuticula"; below this come the circular muscle fibres of the somatic musculature. Deeper still are gland cells, amongst the longitudinal muscles, and parenchyma cells.

There are three chief views as to the nature of this "investing membrane": (*a*) It is a metamorphosed, cellular epidermis (Zeller, Ziegler, Biehringer, Braun, etc.), nuclei have been stated to occur in it in various members of the group (*Gasterostomum*, *Amphistomum*, *Monostomum*), and in cercariae the nucleated epidermis is stated to become a cuticle. (*b*) It represents a basement membrane, the true epidermis and cuticle having been cast off (Schneider, Kerbert); this view is founded on the fact that, during the development of Malacocotylea, an external layer of ciliated cells is shed, and in later stages a cuticle-like membrane remains. (*c*) The investing membrane is a cuticle in the same sense as that of a Chaetopod. But here again differences of opinion as to its origin exist: (α) Some believe that the "subcuticula" serves as its matrix, and represents an epidermis which has lost its cellular character; (β) others regard this "intermuscular subcuticula" as the most external layer of the parenchymal tissue (Braun, etc.), and that the gland cells alone are the representatives of the epidermis.

Recent studies by Blochmann (8, 9) and Kowalevski (23) upon the structure of Cestodes and Trematodes go to show that the investing membrane consists of two parts—the greater part of it represents a true cuticle, while the lowest layer is a basement membrane (Fig XIX. 2). The epidermis which is more clearly seen in some Cestodes (*Ligula*) than in Trematodes is represented by deep-lying cells, some of which are glandular, with narrow necks traversing the basement membrane; the cells of the epidermis have, however, become separated from one another by the upward growth of the parenchymal tissue and muscles, just as in *Hirudo* (Lankester, 25) and in some Oligochaeta (Benham, 6) the blood-vessels with connective tissue invade the epidermis and, penetrating between the cells, break up the layer; in these Annelids the cells remain attached to the cuticle by a broad external end; but in Trematodes the invasion of tissue has gone so far as to leave only a very narrow part of each cell in connection

with the cuticle; and at the same time, the basement membrane has been pushed upwards against the cuticle; the cells have, so to speak, slipped down through this membrane.

It is worthy of note that Max Braun has observed a definite external layer of cylindrical cells in the lateral suckers of *Nitzschia* and *Epibdella*, they are not covered by a cuticle, which stops abruptly against the cells.

The constitution of the parenchyma (or mesenchyma) also presents difficulties of elucidation; by most authorities it is regarded as consisting of more or less highly vacuolated, granular, nucleated cells; the extent of the vacuolation differing in different genera, and in different parts of one and the same worm (see Walters, 47). On the other hand, it has been more than once suggested, and recently again by Blochmann, that these vacuoles are intercellular, the cells themselves being extremely branched.

The musculature retains the same arrangement as in Turbellaria, but the large "myoblasts" give rise not to one muscle fibre, but to many.

In the Trematoda the necessity for fixation which is effected primarily by the posterior sucker, appears to have led to a forward movement of the generative pores in most forms, as well as of the excretory pore in Heterocotylea, and in the former point the Class contrasts with the Turbellaria. The peculiar secondary adhesive apparatus of Holostomidae is clearly antagonistic to this forward position, and we find the genital pore at the posterior end, which must be regarded as secondarily acquired by them.

The mouth, however, retains its ancestral position at the anterior end of the body. It leads into a buccal cavity, upon which follows a *pharynx bulbosus*. The intestine has lost its primitive, sac-like shape, owing to the forward and central position of the generative organs. Coincidently with the great development of these, the dorsal and ventral walls of the intestine have coalesced as in many Turbellaria (cf. the origin of radial and circular canals in Medusae), and in great part disappeared, so that two main limbs, one on each side, remain. Nevertheless, this obliteration of the central region has not occurred in the Aspidocotylea or *Gasterostomum*, and only incompletely in many Heterocotylea, where the two forks are united by transverse caeca (as *Polystomum*). In this and other instances, too, the intestine resumes its median position behind the gonads (Fig. II. 2, 4). The reticular gut of the Polystomea is therefore more primitive than the simple, bifurcated intestine of such forms as *Calicotyle*, *Tristomum*, and most of the Malacocotylea. This view is supported to some extent by the fact that in the young *Polystomum* the central intestine is a simple sac which only exhibits its characteristic form during the appearance of the gonads (Fig. V. 7). In other forms, also,

whose development has been followed, the intestine is at first sac-like. The two main limbs may also carry lateral caeca, which appear to have developed independently of those in Triclads and Polyclads, and which ramify amongst the lobes of the laterally placed vitellaria. It is necessary to point out that the intestine of *Distomum hepaticum*, with its multitude of branching caeca, is quite exceptional amongst the family Distomidae, and, indeed, amongst the Malacocotylea; for in this order the gut is characteristically bifurcated, though the length of limbs may vary in different species.

The excretory system presents little of the network character seen in many Turbellaria; the arrangement of the canals and the position of the pores is seen in the diagrams. Apparently, the primitive position of these pores is not posterior; separate pores exist in cercariae and rediae; the median pore of the adult Malacocotylean and *Aspidogaster* being due to a fusion of the right and left ducts.

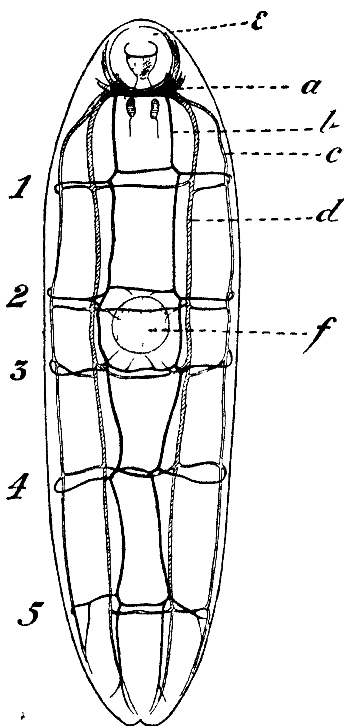


FIG. XX.

Nervous system of *D. cylindraceum*, as a type of that of the Malacocotylea (from Looss). The animal is viewed from above. *a*, brain; *b*, dorsal longitudinal nerve stem; *c*, lateral nerve; *d*, ventral nerve. These three stems are connected by the circular commissural nerves, 1-5. *e*, anterior, *f*, ventral suckers in outline.

With regard to the nervous system, which in its main lines was first correctly recognised by Ramdohr (1814), a comparison of the figures will show that in the Heterocotylea a more primitive arrangement persists than in the Malacocotylea, in which there is a remarkable constancy of longitudinal stems and circular commissures (Figs. XX. and XXI.).

Some of the ectoparasitic forms, as well as the free larvae of the endoparasitic forms, possess "eyes" which, however, compared with those of Turbellaria are in a degenerate condition. The cap of pigment is directed externally, and embraces a spherical refringent body or "lens," which in its turn abuts upon a ganglion cell, a branch of which runs to the brain. There is nothing which can be

regarded as a retina, and Goto has suggested that they serve in the Heterocotylea as "organs of temperature."

The generative system presents a somewhat greater complication than in the most elaborate Turbellaria, but is built up essentially on the same plan; the female gonad being, except in *Gyrodactylus*, composed of germarium and vitellarium. The male and female ducts, with rare exceptions, open together into an "atrium genitale," and the penis is frequently armed with spines. In the Malacocotylea the original pair of testes persists, and with very few exceptions, such as *D. hepaticum*, each testis is a compact, rounded body. In the Aspidocotylea and Heterocotylea one of the original pair has disappeared, the remaining gland which is provided with only one duct, may remain compact (Fig. IV. 2), or

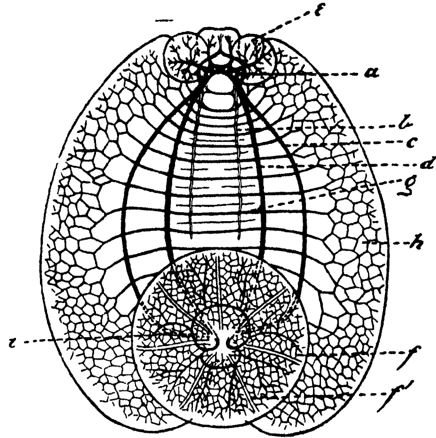


FIG XXI.

Nervous system of *Tristomum molae* (after Lang), as type of that of Heterocotylea, viewed from the ventral surface *a*, brain (on which rest the four eyes indicated by white dots), *b*, dorsal nerve stem, *c*, lateral, *d*, ventral The ventral stems are united by a series of commissures, which are continued on to the lateral nerve, 13-15 in number (*g*) From the brain, on each side, a nerve goes to "prostomium," a second to the sucker These are joined by a ring-like commissure, arising from the stem common to the posterior nerves The lateral and ventral nerves unite in the posterior sucker and are connected by a couple of semicircular commissures, and give rise to network in wall of sucker *h*, marginal network of body, *e*, lateral anterior sucker, *f*, posterior sucker, *f'*, radii

become subdivided by ingrowths of connective tissue into a few large lobes (*Epibdella*), or more generally into many small ones (Fig. II. 2, V. 2), so as to assume the "follicular" condition present in many Turbellaria.

The male copulatory apparatus varies considerably in details of its structure, but these may all be reduced to two types: (1) The word "cirrus" is used for the terminal, eversible part of the sperm duct of *Distomum* and others which projects from the bottom of the male antrum, and is enveloped in the "cirrus sac," containing glands; hooklets are borne along the wall of the duct, and on eversion come to project outwards. A cirrus is rare amongst the Heterocotylea, being met with in *Tristomum* and *Epibdella*. (2) A "penis," such as occurs in the Holostomidae, and in the majority of the Heterocotylea, and in Aspidocotylea, is a specialisation of the terminal region of the sperm duct which

traverses a papilla arising from the floor of the atrium. When in use, this papilla is merely *protruded* through the genital pore. The penis is formed of two parts: (*a*) a muscular, connective tissue sheath, enveloped in a membrane; and (*b*) distally a chitinous armature, either in the form of a crown of hooklets, lying on the outer surface of the papilla, and projecting therefore into the atrium and not into the sperm duct, or a tube. In a few instances (*Udonella*, *Diplozoon*, and some species of *Distomum*) there is no penis or cirrus, and there is every reason to believe that self-fertilisation occurs.

The germarium is single, the germ duct or oviduct is short, extending as far as the special dilated region known as "ootype," into which the shell glands open; into the oviduct there open the vitelline ducts from the vitellarium, which is follicular or distinctly lobed, except in *Udonella* and *Calceostoma*, where it is compact. In *Diplozoon* it is unpaired, in the rest paired, it always lies dorsal to intestine, against which it is closely placed. Beyond this point the "oviduct" is known as "uterus,"[1] and passes forwards, usually in a more or less undulating course, to the atrium genitale, or in rare instances to its own separate aperture.

But in addition to these organs there are certain ducts, the homologies of which have been much discussed (Fig. XXII.) (1) In the Heterocotylea there is typically a paired, or in other cases a single *vagina*, the opening of which varies in position in different genera (cf Figs I., II, III, V) It is usually ventral, but in *Hexacotyle* dorsal; the single vagina appears, in some cases at least, to be derived from the fusion of two, for in *Axine heterocerca* the single (dorsal) pore leads into two ducts (Goto). In *Polystomum* each vagina opens through twenty or thirty small pores situated on the "lateral swelling." At its internal end the vagina (XXII. 3, *k*) communicates with the transverse vitelline ducts, and in its course is sometimes dilated to form a "spermatheca", the vagina is the female copulatory organ for the reception of the penis; its pore is the "copulatory pore."

The uterine pore may, therefore, in opposition thereto, be termed the "birth opening."

(2) In the Heterocotylea there is also a narrow duct passing from the oviduct, opposite the entrance of the vitello-duct, to the right limb of the intestine. This "genito-intestinal canal" (*f*) whose true relations were discovered by Ijima, and since confirmed by Goto and all who have examined the matter, was originally called the "internal vas deferens" by v. Siebold, and believed to be connected with the testis, close to which it passes; it was then looked upon as a means for direct, internal self-fertilisa-

[1] Goto finds cilia on the uterine epithelium of several genera of Heterocotylea and in the vagina of *Calicotyle*.

tion. It appears to serve for the conveyance of superfluous yolk to the intestine, where it will serve as food.

(3) In the Malacocotylea and Aspidocotylea there is *no vagina*, a fact that is associated with the much greater size of the uterus,

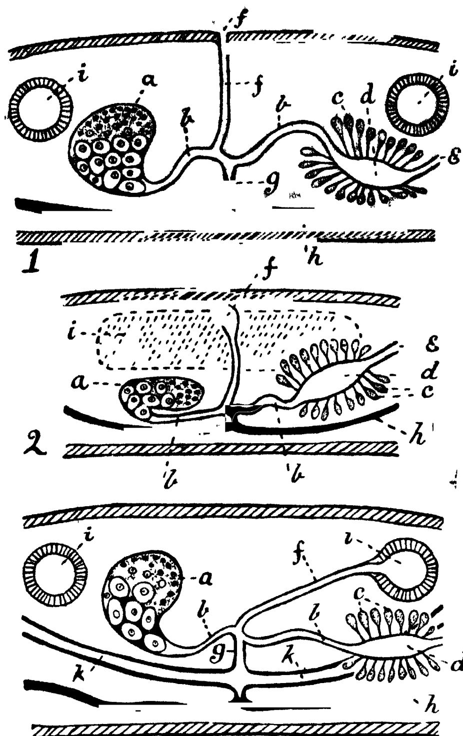


FIG XXII —Diagrammatic Transverse Sections to show the Relations of Various Parts of the Female Ducts in the Three Orders of Trematoda

1 —A Malacocotylean, showing Laurer's canal (*f*)

2 —An Aspidocotylean The "yolk receptacle" (*f*) arises from the oviduct in the same position as does Laurer's canal

3 —A Heterocotylean (the lowest figure) The canal (*f*) is here called "genito-intestinal canal" The right and left *vagina* (*kk*) are represented as entering the median vitelline duct (*g*) In some cases they join the transverse vitelline duct; one or both may be absent In all the figures —*a*, germarium, showing the distal syncytium and proximal germ cells, *bb*, germ duct or duct between the germarium and ootype, *c*, shell glands set round (*d*) the ootype, whence the duct is continued as uterus (*e*); *g*, median vitello-duct, *h*, right and left transverse vitello-ducts, *i*, intestine, which in Fig 2 is represented dotted; "Laurer's canal" passes upwards behind it (see Fig VIII *g*)

These organs do not lie in one plane, the figures represent "projections" in a vertical plane

which contains a very much larger number of eggs than in the Heterocotylea, and often comes to lie behind the testes. Nor is there a connecting canal between the vitelline duct and the intestine, but in place of it there is a narrow canal, first dis-

covered by Laurer (1830), and since known as "Laurer's canal" (Stieda. 1867), which passes up from the oviduct, in the neighbourhood of the ootype, to the dorsal surface, upon which it opens by a minute pore (Fig. XXII. 1, *f*). It has been till recently regarded as the homologue of the vagina of Heterocotylea; but it does not function as such, it is much too small for the insertion of the penis, and although spermatozoa have been observed in it (Looss, 31), they are passing *outwards*, in which they are aided by the current produced by the cilia lining the canal; yolk granules also occur. Recently both Looss and Goto independently have brought forward various arguments from comparative anatomy tending to show that Laurer's canal of the Malacocotylea is the homologue of the "genito-intestinal canal" of the Heterocotylea, which has lost its connection with the intestine and come to open to the exterior; for it would be manifestly less important for an endoparasite to make use of its yolk as food than for an ectoparasite.

(4) In Aspidocotylea the duct leading to the "receptaculum vitelli" agrees closely with Laurer's canal and the genito-intestinal canal, except that it ends blindly below the dorsal integument (Fig. XXII. 2); and there is little doubt that these three canals are homologous.

The eggs of the Trematoda which are operculate, are of various shapes and have a certain systematic value; in the Malacocotylea they are very numerous, much smaller than in Heterocotylea, and rarely have the filament which is so usually present in the latter order, since in the endoparasitic forms they are generally discharged to the exterior and not attached to the host, as in ectoparasitic forms. In a few instances, however, one filament exists, as in *Bilharzia* and species of *Distomum*, or less frequently two in *D. constrictum*, *Monostomum verrucosum*, *Opisthotrema cochleare*.

Historical.—The earlier writers, who concerned themselves chiefly with the liver-fluke, frequently confused the excretory canals with the intestine; thus Carlisle, having injected the former, described it as the latter, the excretory pore being termed "porus ani" Even after the true mouth and intestine had been correctly recognised by Ramdohr (1814), and by Bojanus (1817), there was a general belief that the excretory pore served as an anus, and that the excretory canals were in connection with the intestinal caeca, and acted as a kind of vascular system; indeed, Blanchard (1847) described the contractile bladder as a "heart," and went so far as to deny the existence of a posterior pore. Bojanus (1821) was the first to establish the absence of an anus, though even v Baer (1827) mistook the excretory pore of *Aspidogaster* for the mouth.

The excretory system, even after it had been differentiated from the enteric system by Bojanus, and by v. Siebold, who pointed out its true function, was variously regarded as (*a*) respiratory by Meckel (1846), who sug-

gested that the canals absorbed water through the skin and passed it out through the pore; or (b) as lymphatic, or vascular, in part at least; even Villot, 1882, takes the view that it serves for excretion, absorption, respiration, and circulation. The main course of the canals was known to Laurer and to Mehlis (1831) The fact that the bladder and canals form part of one system was first pointed out definitely by P. J. van Beneden (1852). The movement of the contained fluid was caused, according to Ehrenberg (1835), by valve-like folds, endowed with the power of oscillation; but in the next year v. Siebold rightly showed that it is due to the action of cilia.

The finer structure was investigated by Fraipont (16), who described the "flame cells," but believed them to be in communication, not only with the tubules, but also with the spaces in the parenchyma; this has, however, been shown to be erroneous.

The brain and the main nerves were first accurately localised by Ramdohr; but Otto, 1816, contended that the vitelline ducts, longitudinal and transverse, were the true nervous system, and described ganglia at their junction. Our knowledge of this system is due primarily to Lang (24) and Gaffron (17).

The hermaphrodite nature of the Trematodes appears to have been recognised by Muller; but for a long time the ventral sucker was interpreted as the "birth pore," till Nitzsch (1819) discovered that the sucker is imperforate. The penis was known to Rudolphi, and the common genital pore was held to belong only to the male ducts

V. Siebold was the discoverer of the fact that the egg-producing organ is distinct from the yolk-forming gland.

Relations of the Group—Parasitism.—It is almost an axiom that parasitism leads to degeneration of the parasite, and this usually in an extreme degree; but in the Trematodes this degeneration is scarcely recognisable; for beyond the absence of the ancestral locomotor organs, viz. the cilia of the outer surface, it is scarcely possible to point to any sign of degeneration common to the group. Degeneration of the sense organs is another characteristic of parasites, and although eyes are frequently present in the Heterocotylea, they are less elaborate than in the majority of Turbellaria; and in Malacocotylea they are absent, except in the free-living miracidium and cercaria. The nervous system shows no essential difference from that of Turbellaria, though in the Malacocotylea the peripheral stems and commissures are more definitely arranged.

The generative organs, too, agree with those of many Rhabdocoele Turbellarians, and the alimentary canal is well developed in all members of the group.

The cuticle, as has been suggested, has been developed in relation to the parasitic habit, and *Temnocephala* forms an interesting link between the Turbellaria and Trematoda in this respect.

The suckers so frequently associated with parasitism, and so eminently characteristic of the group, seem to be the cause rather than the result of parasitism, for such relatively small animals as

Dactylocotyle and other ectoparasitic forms would soon be carried away by the current of water passing over the gills of the fish; and *Amphistomum*, or other internal parasites, would be driven down the alimentary tract of its host, by the passage of food, unless they were able to adhere in some way to the host; the modification of the musculature of the body wall is the simplest method of adhesion.

But suckers occur, though of a very simple kind, in many Polyclad and several Triclad Turbellaria, and large ones in *Temnocephala*, so that even these characteristic organs are not in reality novelties or peculiar to the class. It does not appear possible to regard the suckers of Trematodes and Turbellaria as truly homologous; they are rather homoplastic, for they vary in position and relation in both groups. Indeed, but for the absence of cilia, there is no essential difference between a Trematode and a Turbellarian, and there is little difficulty in deriving the former from some Rhabdocoelous form of the Turbellaria, which had taken to the habit of temporarily associating itself with a definite animal, as the Triclad Bdelluridae do at the present day. As this habit became fixed, the means of attachment became improved, resulting in a single posteriorly placed sucker. The animal was thus able to live permanently on its host, and having a ready supply of food at hand, in the host's blood and mucus, took to sucking it, for which purpose a second sucker in the neighbourhood of the mouth would aid the parasite during the use of the "pharynx bulbosus," which acts as an aspirator. The two characteristic suckers having been developed, each became modified in different directions. The anterior sucker became double in the ectoparasitic forms; the posterior sucker became more elaborate, or hooklets were developed to aid in adhesion.

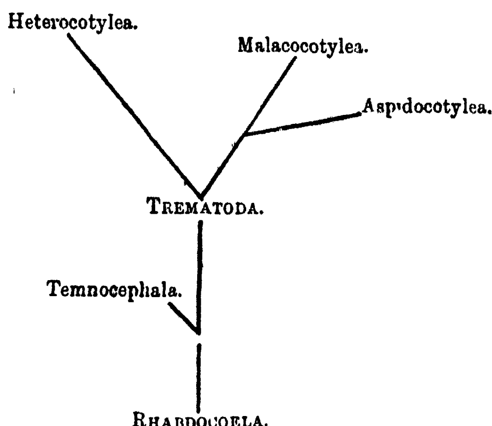
It is customary to look on the Malacocotylea (Digenea) as more highly developed than the Heterocotylea, and as probably derived from them. This view, no doubt, depends on the endoparasitic habit of the former order, and on the fact that the host is a vertebrate, and that the life-history is a complicated one But Looss is of opinion that, on the contrary, the Heterocotylea are the higher order. But if the anatomy of each order and of Rhabdocoelida be compared, organ for organ, with one another, we shall have to take a middle position and look upon the two orders as diverging at a very early stage in phylogeny.

Very possibly some *Temnocephala*-like form was the ancestor of the Trematoda—a form, as said above, with a posterior sucker, but without the anterior ones; the intestine was sac-like, and no doubt the genital organs posterior to it.

The assumption of ectoparasitic and endoparasitic habits, with the anterior suckers or sucker differently arranged, led to a diver-

gence along two lines, in one of which a complicated life-history gradually took place; from this line the *Aspidocotylea* branched off, and possibly the apparently primitive characters of the alimentary canal is one of atavism.

The following "tree" represents the history of the group:—



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CHAPTER XIX.

PLATYHELMIA—CESTOIDEA.

CLASS IV. CESTOIDEA

GRADE A. CESTOIDEA MONOZOA.

Order 1. **Amphilinacea.**
,, 2. **Gyrocotylacea.**
,, 3. **Caryophyllacea.**

GRADE B. CESTOIDEA MEROZOA.

BRANCH A. DIBOTHRIDIATA.

Order 1 **Pseudophyllidea**
Fam. 1. Bothriocephalidae.
,, 2. Solenophoridae.
,, 3. Bothriomonidae.
,, 4. Leuckartiidae.
,, 5. Triaenophoridae.

BRANCH B TETRABOTHRIDIATA.

Order 1. **Tetraphyllidea.**
Fam. 1. Tetrabothridae
,, 2. Gamobothridae

Order 2. **Diphyllidea.**
Fam. Echinobothridae.

Order 3 **Tetrarhyncha.**
Fam. Tetrarhynchidae.

Order 4. **Tetracotylea.**
Fam. 1. Ichthyotaeniidae.
,, 2. Echinocotylidae.
,, 3. Taeniidae.
,, 4. Mesocestoididae.

THE class Cestoidea, as known at the present day, may be defined as follows.—Platyhelminths in which an internal parasitic habit has led to the disappearance of the alimentary canal from every stage in the life-history. The ciliated covering, as well as

definite organs of sense, are likewise absent in the adult. The epidermis, which has sunk into the parenchyma, secretes a thick cuticle, as in the Trematoda. In the parenchyma certain lime-secreting cells are developed in greater or less number. Organs of fixation are developed in a characteristic but varied form at one extremity of the worm.

The egg gives rise to a six-hooked embryo or "onchosphere," which gains an intermediate host; from it some form of "bladder-worm" is usually developed, which has to reach a vertebrate as a final host, in order to attain maturity.

Historical Account.—There can be little doubt but that tapeworms have been known to mankind from very early times, for those infesting domestic animals are sufficiently large to catch the least observant eye; and even such "bladder-worms" as *Cysticercus cellulosae*, *C. tenuicollis*, and *Echinococcus* must have been met with, and recognised as foreign bodies, in the carcases of animals slain for food or sacrifices. Moses probably was acquainted with them, when the pig, rabbit, and hare were forbidden to the Jews. The Greeks gave the expressive name χάλαζαι (= hailstones) to these "hydatids," and some authors refer to the method, still employed, of examining the tongue of the living pig in order to ascertain their presence. The tapeworms were termed ἕλμινθες πλατεῖαι and Aristotle was aware that they were attached to the wall of the intestine, whereas the nematodes or στρογγύλαι were free therein. At an early period (1592) at least two different cestodes were distinguished as inhabiting man (*Taenia* and *Bothriocephalus*), and in the latter half of the seventeenth century the tapeworms and bladder-worms of domestic animals, and later of wild animals killed for food, etc., began to receive attention. But for a long time, even after a considerable number of naturalists had been working on the subject, the relation of these two stages was unknown, or only vaguely guessed at, till Pallas and Goeze recognised that the head contained in the bladder-worm is capable of evagination on compression, and resembles the head of certain tapeworms. The earlier systematists (Zeder, Rudolphi) separated the bladder-worms, or "Cystica," from the tapeworms, or "Cestoidea," as distinct orders; but Blainville and Dujardin united the two groups, as being related to one another. P. J. van Beneden rightly regarded the "Cystica" as some normally occurring stage in the life-history of the "Cestoidea." Von Siebold, on the other hand, had put forward the theory that the bladder-worm is some stage in the history of a tapeworm which has gone astray in the wrong animal, and, undergoing hydropic degeneration, is destined to die, unless this animal is eaten by the proper host, when the bladder-worm will not only live in the intestine of the host, but will give rise to a tape-worm. This idea of von Siebold's received considerable support

from Dujardin, Leuckart, and others; but the matter remained one of mere speculation till 1851, when Küchenmeister, a medical man of Zittau, commenced a series of experiments in feeding suitable animals with bladder-worms. Thus, he mixed a known number of *Cyst. pisiformis* from the rabbit's omentum with the food of dogs, and he obtained after a time a number of specimens of *Taenia serrata* from their intestines. Similarly, he demonstrated that *C. cellulosae* from the muscles of the pig gives rise to *Taenia solium* when swallowed by man; and that the small heads removed from *Coenurus cerebralis*, which lives in the brain of sheep, develop, when fed to a dog, into *Taenia coenurus*. He then caused the ripe proglottids of this worm to be swallowed by a sheep, which a month later had an attack of "staggers." It was killed, and fifteen small coenuri were found in its brain.

These and other experiments placed the relations of the "cystic worm" to the "tapeworm" on a firm basis, and were soon followed by others, undertaken by von Siebold (43), Leuckart, van Beneden, whereby it was proved beyond doubt that the bladder-worm or hydatid is an essential stage in the development of those tapeworms, from the eggs of which they arise. Further, it became evident that two different animals, or "hosts," are necessary for the completion of the life-cycle, the bladder-worm occurring in some definite intermediate host, which forms the prey or food of the final host, in which the bladder-worm develops into the tapeworm.[1] It was recognised that "cystic worms" occur in the muscle, connective tissue, and various viscera, other than the alimentary canal (of herbivorous animals as a rule), and that the adult tapeworms always live in the alimentary canal (of carnivorous animals as a rule).

But still other problems remained for solution, especially that which Steenstrup's famous theory of "alternation of generations" had suggested, and this and other matters are dealt with at the end of this chapter, as some of these details are still matters of controversy.

Among the more important writers on the classification and description of new genera and species, the following may be mentioned:[2]—Redi (1687-1705), Pallas (1781), Goeze (1782), Rudolphi, Zeder, Dujardin (1845), E. Blanchard (1847), P. J. van Beneden (1849), Diesing, Krabbe, Linton, Stiles, Raillet. The anatomy of various forms has received particular attention at the hands of Blanchard, Wagener, von Siebold, and

[1] In a few instances there is, however, no change of hosts, but merely a change of organs in one and the same host. The best known case is that, *H. murina*, elucidated by Grassi, where the cysticercoid occurs in the villi of the intestinal wall, the strobila in the cavity of the same intestine. Von Linstow has found the larvae of *Tetrarhynchus longicollis* in the same fish as the adult, and so for *Triaenophorus nodulosus*.

[2] For a complete historical account and bibliography, see Bronn's *Thierreichs, Würmer*, by Max Braun

especially van Beneden, whose work on Fish Tapeworms (2), like Leuckart's great work on the Parasites of Man (22), is a storehouse rich in facts. Among more recent writers mention may be made of Sommer and Landois (44, 45), Zschokke (52), Pintner (32-34), Monticelli (30), and others, to whom reference is made below.

The life-history of various genera has been gradually elucidated by the researches and discoveries of von Siebold, Wagener (49), E. and P. J. van Beneden, Leuckart (21), Kuchenmeister, Moniez (28), Schauinsland (40), Grassi and Rovelli (13), Villot (48), and others. Among the more important steps in anatomical discovery, which have led to our knowledge at the present day, are the following —The head or scolex of a dog tapeworm was discovered for the first time by Tyson (1683), of *T. saginata* by Audry (1700), of *Bothriocephalus* by Bonnet (1777), and of *Cyst. cellulosae* by Malpighi. The suckers, at first regarded as "eyes and nose," were correctly interpreted by Redi. The isolation and independent movement of the proglottids or *vermes cucurbitini* were known to von Siebold. The fact that eggs were laid by the proglottids was observed by Leeuwenhoek (1722) Hermaphroditism of the joints appears to have been known to Werner (1782), but the accurate determination of the constituent parts has been very slow and gradual. On an isolated proglottid of *Taenia*, the uterus, full of eggs, and the more or less prominent genital pore on its margin, were the first to receive attention, and were, by many zoologists, mistaken for intestine and mouth respectively (Linnaeus, Dubois) But Goeze and Pallas, recognising the contents as eggs, concluded that the uterus was an "ovary." This was set right by the discovery by von Siebold of a "germarium" and a "vitellarium" in certain forms; but to Leuckart belongs the merit of tracing out the ducts connecting the various parts both of the male and of the female system, though even some of his interpretations were shown by Sommer to be erroneous (thus he mistook the vitellarium for a germarium, and *vice versa*), and it was Sommer who has given us the best descriptions and drawings of the structure of a proglottid in *Taenia* and in *Bothriocephalus*, while Zschokke has extended this knowledge in other forms The testes were discovered by F. E Schulze in 1820, and the copulatory organs by Platner in 1859. The genitals of the Tetraphyllidea were accurately described by van Beneden. The excretory system, originally identified by von Siebold (1838), was regarded by Blanchard as a part of the alimentary system. It was followed out in its main course by van Beneden in a number of fish tapeworms. Its histological structure has been investigated by Fraipont, Pintner, Poirier (35), and Kohler (18) amongst others.

The nervous system, which was first noted by J. Muller (1836), has been studied by Lang (20), Niemec (31), and recently by Tower and Luhe; the "brain" having been already recognised by Wagener. The structure of the parenchyma, skin, etc, has received considerable attention in recent years, the most modern writers on this subject being Zernecke (51) and Blochmann.

In the majority of the Cestoidea the body is metamerically segmented, the reproductive organs sharing in this segmentation;

but there are certain genera which consist of a single segment and have only one set of genital organs. This group of forms only differs materially from certain Trematodes in the absence of the enteric cavity, and constitutes a lower grade, from which the segmented Cestodes are derived.

This grade is the *Monozoa*, and the second grade may be termed the *Merozoa*.

GRADE A. CESTOIDEA MONOZOA, Lang (= *Cestodaria*, Montic.; = *Cestodes monogenèses*, v. Ben., = *Atomiosoma*, Montic.).

Cestoidea, in which the animal consists of a single segment, containing a single set of reproductive organs. In addition to the male pore and female (vaginal) pore, there is a third aperture, that of the uterus (birth-pore). The apparatus by which fixation is effected consists, usually, of a single sucker, but presents considerable variation in form, as well as in disposition, with regard to the genital pores.

ORDER 1 **Amphilinacea.**

FAMILY 1 AMPHILINIDAE. Oval or leaf-shaped, without a distinct "head"; with a single small acetabulate sucker at one end *Amphilina*, Wagener; *A foliacea*, Rud, in the sturgeon (see 39), (Fig II 1); *A liguloidea*, Dies, in fresh-water fish, Brazil; *Wagneria*, Montic; *W. proglottis*, Wagn., in the intestine of *Scymnus nicaeensis.*

ORDER 2 **Gyrocotylacea.**

FAMILY 2 GYROCOTYLIDAE. Leaf-shaped, with crenate margins. At the pointed extremity is a small but deep sucker; at the opposite end is a "rosette organ" carried by a cylindrical peduncle, traversed by a canal opening at each end, from which a peculiar proboscis-like organ can be everted. *Gyrocotyle*, Dies. (= *Amphiptyches*, Wagn), (see 46), in the intestine of *Chimaera* and *Callorhynchus* (Fig II. 4).

ORDER 3 **Caryophyllacea.**

FAMILY 3 CARYOPHYLLAEIDAE Elongated, cylindrical worms, either with a single sucker or without one, and then with one end capable of considerable mobility. *Monobothrium*, Dies., with a single terminal sucker; *M. tuba*, Wagn, in the intestine of *Tinca chrysitis; Caryophyllaeus*, Mull, without a sucker, but with a characteristic mobile organ, capable of being thrown into undulatory folds, giving the appearance of a "clove-pink"; *C. mutabilis*, Rud (Fig I.), in the intestine of Cyprinoid fishes, and (young) in the coelom of *Tubifex*, in segments 8 to 20 (see 50). The worm described by Leuckart as *Archigetes sieboldii*, from the genital segments of *Tubifex rivulorum* (see 23), is in all probability only the immature phase of *Caryophyllaeus.* The cylindrical body carries a tail provided with three pairs of hooklets, thus resembling the "caudal vesicle" of such a Cestode as *Taenia solium*, it has been suggested that it is a permanent "cysticercus form" with the head everted. The head

is known only from Leuckart's observations on preserved material. This worm is stated to become sexually mature in the Oligochaete, and would be remarkable, firstly, for being the only Cestode inhabiting a single host, and secondly, in that host being an Invertebrate. The genital organs (see 15) appear to be identical with those of *Caryophyllaeus*, and it is desirable to have further information about the character of the "head,"

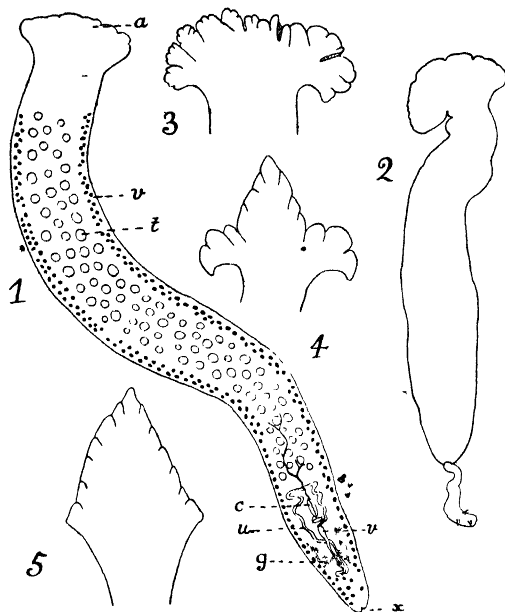


FIG I.—*Caryophyllaeus mutabilis*, Rud

1 —Mature worm from the intestine of the roach, *Leuciscus rutilus* (×7½, orig) The general disposition of the genital organs is shown *a*, mobile organ, *c*, cirrus, *g*, germarium, *t*, testes, *v*, vitellaria, *u*, uterus, the coiling of which has been simplified, *v*, vagina, *x*, excretory pore The male duct opens into the atrium (the outline of which is unfortunately indistinct) *opposite* to the vagina, and the uterus opens also into the atrium, close to the latter. The atrial pore is not lettered, but is seen in line with the letter *u*

2 —Immature worm removed from the coelom of the genital segments of *Tubifex rivulorum* (×15, orig) It still retains its "caudal vesicle," which is armed with six hooklets This specimen is a small one; others occur in the Oligochaete of the same size as, or even larger than some specimens found in the fish, and frequently have the genital organs fully formed, but without eggs

3, 4, 5 —Outline of the mobile organ in three stages of forward movement—3, at the beginning, and 5, at the terminal stage of the process During this movement of the mobile organ, a wave of contraction passes forwards along the body, so as to bring the whole animal forwards

for in preserved specimens of the latter genus, an appearance, not unlike that figured by Leuckart, is presented It is, moreover, to be noted that the genital organs of *Caryophyllaeus* are fully developed while it is still provided with a "caudal vesicle" and inhabiting the body of *Tubifex*.

Remarks upon the Monozoa.—These unisegmental Cestodes exhibit undoubted affinities with the Trematodes, and especially with the Heterocotylea. A résumé of the anatomy of the genera

included will be found in (30). Of the various genera included in the grade, it is *Amphilina* that appears to be the most primitive in its anatomy, though Leuckart sees in "Archigetes" an archaic form; but in its general anatomy there is here a greater divergence from the Trematodes than is seen in *Amphilina.*

It is usual to regard the single sucker of all these genera as homologous throughout, and to place it anteriorly; but if we have regard to its position in relation to the genital pores, it is possible to deny this homology. Spencer (46) and Lonnberg, though without definitely expressing any general dissent from the usual view, place the sucker of *Gyrocotyle* at the posterior end, whereas Wagener and others place it anteriorly.

If we examine the genital organs and ducts in *Amphilina*, on the one hand, and any Heterocotylean Trematode on the other, we shall see that the comparison is very much more easily appreciated if the sucker of the former be placed posteriorly instead of anteriorly as is customary

In *Amph foliacea* the sucker is at the pointed end (Fig. II. 1); the male pore is at the opposite extremity, the penis is armed with ten hooklets; the vas deferens soon bifurcates, and its branches are distributed to the marginal, follicular testes. The germarium is single, the short germ-duct opens into the ootype, which communicates with three canals: (*a*) the short, common vitello-duct; (*β*) the egg-containing duct or "uterus," which is a long undulating canal opening externally close to the sucker, and (*γ*) a short "vagina" or copulatory canal, which opens near the male pore. In *A. liguloidea* there is a fourth canal (*δ*), which runs in the opposite direction and ends blindly, it is known usually as the "anterior vagina."

Now in the Heterocotylean (see Fig. I p. 51) the germarium lies anteriorly to the testes, the sperm-duct and the uterus (or egg-containing duct) run forwards side by side to open near the anterior end of the body, either close together or into a common atrium. The vitellarium is identical in Cestodes and Trematodes, the vitelline duct opening into the oviduct opposite to the junction of the latter with the uterus. Arising close to this point there is in the Heterocotylea the vagina or copulatory duct, whose external pore is independent of the uterine or birth-pore, and generally posterior to it. Moreover, the genito-intestinal canal (Laurer's canal) communicates with the oviduct in the same region. Now, turning again to *Amphilina*, the female copulatory duct or "vagina" has the same topographical relation to the other parts of the apparatus as the "uterus" or egg-containing duct of Trematodes; and the "uterus" of the Cestode corresponds with the "vagina" (when present) of the Trematode. Further, the "anterior vagina" of *A. liguloidea* is

comparable with the Laurer's canal of the Trematode, which has lost its opening (cf. the receptaculum vitelli of *Aspidogaster*).

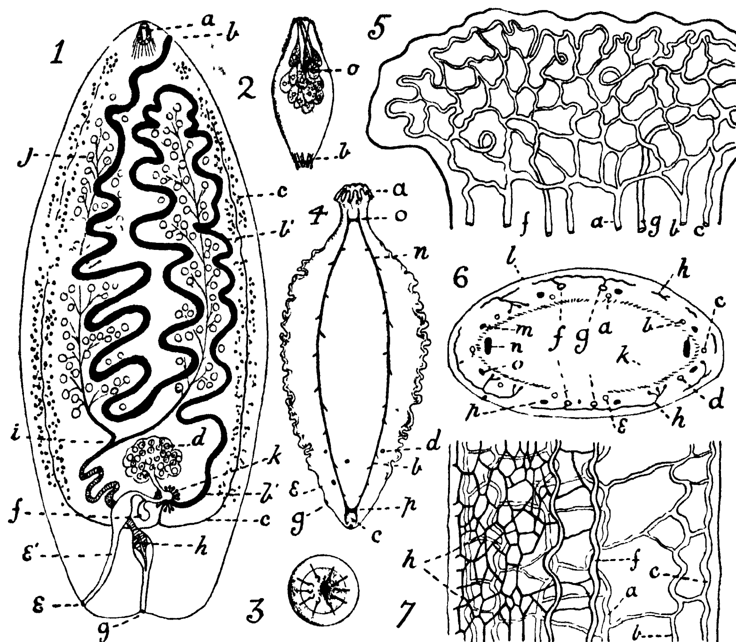


FIG II —Monozoa

1 —Generative system of *Amphilina foliacea*, Rud (combined from figures by Salensky and Wagener), out of the sturgeon *a*, sucker, with retractile muscles (?) or gland cells (?), *b*, uterine or birth pore, *b'*, uterus, *c*, vitellarium and vitellarian duct, *d*, germarium, its duct opens into the ootype, *e*, the vaginal pore, *e'*, the vagina, dilated in its upper part, *f*, spermatheca, *g*, male pore, *h*, cirrus, *i*, sperm duct, which is represented as less convoluted than it is in reality, the wide, convoluted region being the seminal vesicle, *j*, testes, *k*, shell gland

2 —The larva of *Amphilina foliacea* removed from the egg (after Salensky) The upper end is ciliated; the other end is slightly cupped and carries ten hooklets (*b*), *o*, gland cells opening anteriorly.

3 —The same from behind, showing the ten hooklets, arranged round the terminal cup (Orig)

4 —*Gyrocotyle urna*, Wagn Outline of the ventral surface showing external apertures and nervous system (after Spencer) *a*, peculiar frilled organ, *b*, uterine pore, *c*, terminal sucker, *d*, the left excretory pore, the right one is not lettered, *e*, vaginal pore, *g*, male pore on the margin, *n*, lateral nerve, *o*, anterior commissure, *p*, posterior commissure

5, 6, 7 represent the arrangement of the excretory system in *Caryophyllaeus* 5 The mobile organ, dorsal view (Modified from Fraipont) 6 A transverse section of the body (After Will) 7 Dorsal view of body (Orig) *a*, *b*, *c*, *d*, *e*, the five descending canals of one side, these are connected by a network throughout their course, as is shown well in 5 and 7 At the hinder end of the body the ten canals open into a contractile sac *f*, *g*, the "ascending canals" which, in the greater part of the body, lie superficially to the descending canals (6), but in the neck sink into the "medullary region" [In 7 the canal marked "*f*" should be "*g*"] These ascending canals are connected by a fine, superficial network (*h*), which carries numerous flame cells, which are indicated in 6, *k*, the longitudinal, muscular layer separating the parenchyma into a cortical zone, in which the excretory canals lie, and a medullary region containing the genital organs *l*, *m*, *n*, *o*, *p*, the five longitudinal nerve cords of the left side, *n* is the stout lateral or marginal nerve corresponding to that in 4

As was pointed out above (Trematoda, p. 87), the vagina or copulatory duct of the Heterocotylea appears to have no homologue

amongst the Malacocotylea; it is a new structure;[1] whilst the uterus functions in both orders as an egg-containing duct, to which is added in the latter order the function of a copulatory duct. In the whole of the Cestoidea, however, both these ducts can be recognised; but the original uterus is now employed exclusively as a copulatory organ or vagina, whilst the original copulatory organ has lost its function, and, becoming greatly enlarged, serves as an egg-containing duct, which, as we shall see amongst some of the Merozoa, loses its external opening, and becomes a mere blind sac.

If the identification of these parts is correct, and they have the same relative position in the *Amphilina* as they have in the Trematoda, this becomes still clearer on the reversal of the ordinarily assumed position of the sucker, and we may therefore conclude that the sucker of *Amphilina* is homologous with the posterior sucker of Heterocotyleans, and not with the anterior, as is generally assumed.

Gyrocotyle also has a sucker at one end; but in order to bring the genital ducts and pores into agreement with those of *Amphilina* and the Heterocotyleans, this sucker must be placed anteriorly when that of *Amphilina* is posterior. Hence, the suckers in the two genera are not homologous, for that of *Gyrocotyle* corresponds with the anterior sucker of the Trematodes, whilst the "rosette organ" and its peculiar proboscis possibly represents the posterior caudal disc of the latter class. In *Gyrocotyle* this position brings the paired excretory pores anteriorly, as in the Heterocotyleans We cannot at present employ the nervous systems to aid us in comparison, for Spencer and Wagener differ in their identifications of the "brain," which leads to the difference in their mode of orientating the animal. It is less easy to decide the point in *Caryophyllaeus*, for the male and female ducts present quite peculiar relations (Fig. I 1). The male duct, instead of running alongside the vagina as in all other Cestoidea, runs towards it from the opposite end of the body, and the three ducts open into a common atrium. If we place the mobile organ posteriorly, and attempt to homologise it with the rosette of *Gyrocotyle*, we shall have an anterior, median, excretory pore, which position is unknown amongst the Trematodes, though it exists in *Bothrioplana*. At the same time the relative position of testis and germarium becomes that normal in the Trematoda.

This rotation of the axis would lead to the assumptions (1) that the "caudal vesicle" or tail with its six hooks in *Caryophyllaeus*, and therefore in the rest of the Cestoidea, is morphologically anterior, a view already adopted by Grassi, and by Perrier, Blanchard, etc., on quite other grounds; and (2) that the suckers, etc., on the scolex

[1] Looss, however, while taking the above view with regard to the uterus of Trematodes, holds (with Monticelli, Pintner) that the uterus of Cestodes is homologous, not with the vagina, but with the genito-intestinal or Laurer's canal of the Trematodes. While adopting Goto's views it has been deemed advisable in this article to retain the usual names for these various ducts in the Cestodes.

or "head" of the Merozoa are posterior. There seems to be no *a priori* reason why an organ of fixation, varied in character as it is in the Monozoa, should not occupy different positions in the different genera. But although we may conclude that in *Amphilina* the sucker is morphologically posterior, that in *Gyrocotyle* it is anterior, and that the mobile organ of *Caryophyllaeus* is also anterior, it has been considered desirable, while drawing attention to this comparison between the "Archicestode" and the Trematode, to preserve the usual terminology and mode of representation.

The excretory system of *Caryophyllaeus* consists of a superficial network of capillary vessels (Fig. II. 5, 6, 7), bearing numerous flame-cells, and communicating with certain larger canals lying in a deeper plane—the "ascending canals"—of which there are a dorsal and a ventral on each side; they pass forwards into the neck, where they unite to form a single lateral vessel on each side, which enters an elaborate plexus in the mobile organ, from this plexus ten "descending canals" pass backwards, connected here and there by transverse vessels, to open into a median contractile sac at the posterior end of the body, which communicates by a terminal pore, as in the Malacocotylea. This is essentially the plan of this system throughout the class. In "Archigetes" it is stated that there are only eight descending canals. We know nothing of the system in *Amphilina*. In *Gyrocotyle* the system is represented by a network only, without main canals, opening by two pores (as in Heterocotylea), and whereas in the Cestoidea in general flame-cells have been recognised in the outer layer of the parenchyma, Spencer was unable to detect any in *Gyrocotyle*, but many of the larger canals of the excretory system are provided with a continuous row of cilia on one side.

The nervous system in *Caryophyllaeus* consists of a pair of deep lateral nerves, with four dorsal and four ventral more superficial nerves. All are connected anteriorly by a ring-shaped "cerebral commissure," but without special accumulation of ganglion cells here. Anteriorly, nerves go to the mobile organ, and posteriorly the lateral nerves unite around the excretory pore

In *Gyrocotyle* and *Amphilina* (Lang, 20) a more or less laterally placed pair of nerves runs along the body, united at each end of their course

Very little is known about the life-history of the Monozoa. *Caryophyllaeus* passes the earlier part of its life in the coelom of *Tubifex* (D'Udekem, 1855) Here, while retaining a "caudal vesicle" with six hooklets, it grows to a considerable size, and its genital organs become fully developed, though we have no evidence that eggs are fully formed while in this host, as those of "Archigetes" are stated to do; the worm must be swallowed by a carp, roach, etc., when the *Caryophyllaeus* becomes mature in

the intestine of its new host. The eggs are operculate, as in *Bothriocephalus latus*, and do not undergo any development till they are laid. The six-hooked embryo is not ciliated, and feeding experiments have thrown no light on the question as to how the parasite gets into *Tubifex*. In *Amphilina* (39) the non-operculate eggs are provided with a filament at one end, as in some Trematodes. After a development resembling that of a normal Cestode, an oval embryo issues (Fig. II. 2, 3); one half is ciliated, and at the opposite end it carries ten hooks, which, curiously, are precisely like those of the penis in number and shape. There are also in *Gyrocotyle* ten hooks in the embryo A group of unicellular glands opens at the ciliated extremity, which have been regarded with little justification as a remnant of the enteron. It is even doubtful whether they develop into the glands which open into the sucker of the adult. The fate of the embryo is unknown, as is also the intermediate host.

GRADE B. CESTOIDEA MEROZOA (= *Cestodes digenèses*, v. Ben.; = *Cestoda polyzoa*, Lang; = *Tomiosoma*, Montic.).

Cestoidea, in which the adult worm or "strobila" consists of two distinct parts, viz. (1) a sterile head or "scolex," provided with organs of fixation; and (2) a genital region or "body," in which the genital organs are metamerically repeated; and in most cases this repetition is expressed externally by definite constrictions separating the worm into "proglottids," each of which contains usually one set of genital organs. These proglottids in most cases drop off from time to time when mature

It will be convenient to describe a definite type, viz *Bothriocephalus latus*, in order to illustrate the anatomy of the Merozoa in general The "broad tapeworm" (Fig. III 1) of man has a wide area of distribution, but is limited to such peoples as employ uncooked river fish as an article of diet, for in these fish, especially the pike, the early stages of development are passed.

The adult worm or "strobila"[1] consists of head or "scolex,"[1] and a large number of short but broad segments or "proglottids."[1] These are much compressed dorso-ventrally, and broader from side to side than they are long, so that the worm has the form of a band or ribbon, to which fact the technical name for the class is due. The number of proglottids in *B. latus* may be as many as 3000, or even more; and the length of the worm reaches 20 or 30 feet.

The proglottids are not all of the same size or shape; as the proximal region (towards the scolex) is approached they become narrower, and quite far forwards their dorso-ventral diameter or

[1] These terms were introduced by P J. van Beneden, but Dujardin had already used the term "proglottis" for the free, isolated, mature segment of *Taeniae*. Van Beneden, however, used the word in a slightly different sense.

thickness approaches their lateral diameter or breadth. They thus become sub-cylindrical, and at the same time the constrictions between them become gradually less and less distinct, till finally

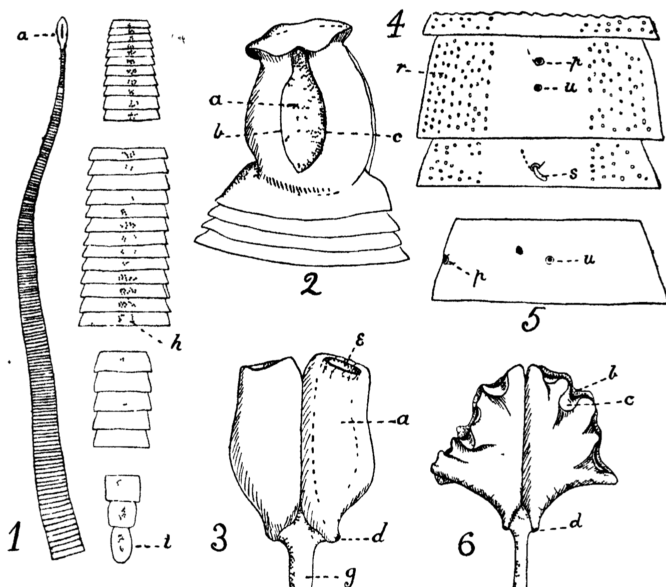


FIG III

1 —*Bothriocephalus latus*, L The proximal part of a strobila, with successive portions from the more distal region (reduced after Leuckart) *a*, the scolex, showing the ventral bothrium *h* indicates the uterus, containing eggs, *i*, terminal proglottid

2 —The scolex of *Bothriote*[illegible] Rud (=*B proboscideus*, Rud) From the salmon (Magn , orig) *a*, [illegible], *b*, *c*, its right and left lips

3 —The scolex of *Solenophorus* (*Bothridium*) *megalocephalus*, Crepl , out of the intestine of python (Magn , orig) It is seen from the side, so as to show the dorsal and ventral bothria, each of which is a tube formed phylogenetically by the union, along part of their extent, of the right and left lips (*b*, *c*) of the bothrium , *a*, the cavity of the tube, the inner margin of the wall being indicated on the right of the figure by dotted lines , *d*, the small proximal opening , *e*, the wide, distal opening, which is provided with a couple of valve-like folds , *g*, the commencement of the strobila

4 —Ventral surface of a proglottid, with portions of two neighbouring ones, of *B latus*, L *p*, The atriopore—copulatory pore common to both male and female ducts , in the lower proglottid the cirrus (*s*) is represented as everted , *u*, the uterine pore , *r*, region of the proglottid occupied by the testes and vitellaria

5 —A ventral view of a proglottid of *Bothriotaenia*, *Disymphytobothrium*, and other genera, in which the atriopore (*p*) is [illegible]

6 —Scolex of *Duthiersia* [illegible] out of *Varanus* (Magn , orig) The lips (*b*, *c*) of each bothrium are united proximally to form a tunnel, the margins of the upper opening are much folded , *d*, proximal opening

they disappear. This region is the "neck," and it is at this point that new proglottids are being constantly formed.[1]

[1] In a few instances, such as *B. punctatus* and a species from Japan, there are apparently intercalated proglottids, as if a proglottid had budded off another one. But this is not the case , it is due to incomplete formation of a proglottid. In some species each young proglottid contains 2-6 sets of genital organs one behind the other, but the adult joint has only one set (Ijima).

The neck bears the head or "scolex," which is usually regarded as the anterior end of the worm, but which is more probably the morphological posterior end. It is here flattened in a plane at right angles to that of the proglottids, viz. from side to side; its dorso-ventral diameter being greatest; the dorsal and ventral surfaces are therefore narrow, along each there is a narrow but deep sucking groove or "bothrium," elongated in the direction of the scolex (Fig. III. 2). The wall of the bothrium consists of bundles of muscles which are not limited internally from the parenchymal tissue (Fig. IV.)

In respect of the general microscopic structure, it is unnecessary to confine ourselves to a type. The body of the Cestoidea is covered by a cuticle (non-chitinous, according to Leuckart, and

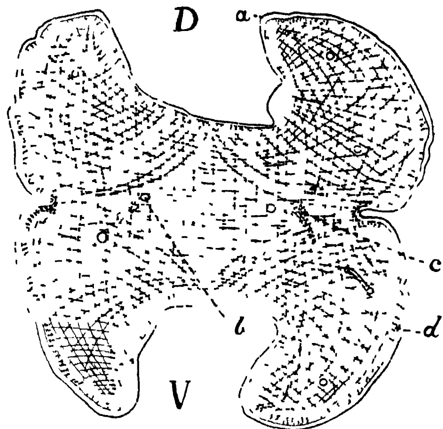


FIG IV

B microcephalus, Rud A transverse section of the scolex (× 50 orig.) *D* and *V* indicate the dorsal and ventral sucking grooves or bothria The substance of the scolex consists chiefly of muscle fibres arranged in three main lines, viz dorso-ventral, transverse, and oblique, the direction of each of which is modified by the outgrowth (*a*) to form the sides of the sucking grooves, *l*, the main excretory canal, branches of which are also shown in various parts of the scolex, *c*, the edge of the ganglion and the uppermost part of the main lateral nerve, with accessory nerves passing away

containing $CaCo_3$) which is of variable thickness. Probably in the primitive Cestodes the cuticle bore small spinelets over the whole surface of the body, as in *Gyrocotyle*, but in the majority these have disappeared from the general surface of the body, and remain only in the cirrus (or penis) of many genera, while in various parts of the organs of fixation they have become greatly enlarged to form hooklets.

The cuticle consists of two to four layers (see Zernecke (51), etc.), the outermost of which generally appears as if composed of short, close-set "hairs," corresponding with the outermost layer of Trematodes, and this appears to be shed periodically (Fig. V.). The deepest layer is always distinguishable as a thin membrane differing from the rest; this is the basement membrane, produced by the parenchymal cells (Blochmann, Trematode literature, 8); the rest of the cuticle is produced by the "subcuticula," and is traversed by fine canals (in *Ligula*, *Taenia*, and others) which contain either

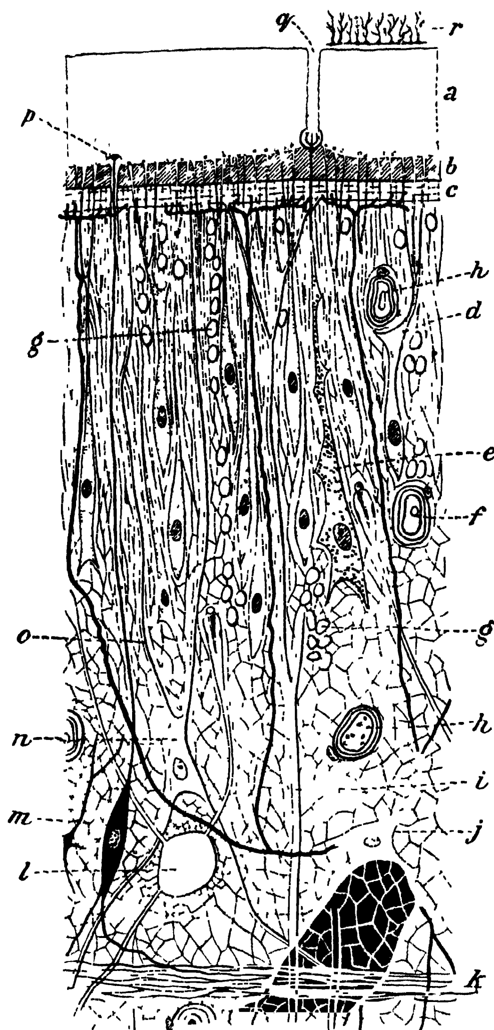


FIG V

Diagram of a transverse section through the body wall of a young *Ligula* (After Blochmann) *a*, cuticle, *b*, basal membrane, *c*, outer circular muscles, *d*, epidermal cells—only a few are represented, each is prolonged upwards through the basal membrane to the base of the cuticle, *e*, a gland cell (*Korbchenzelle*), *f*, a flame cell (the index line unfortunately stops at a lime cell, the flame cell lies a little inside it Another flame cell is shown between the index lines *g*, *o*), *g*, bundle of outer longitudinal muscle fibres, *h*, a calcareous corpuscle, "lime cell," with peripheral nucleus, *i*, dorso-ventral muscle fibre, terminating above in branches amongst the circular fibres, *j*, much branched cell, which Blochmann calls "parenchyma" cell, but its relations to muscle fibres recall a nerve cell, *k*, nerve plexus, *l*, excretory vessel giving off capillaries, terminating in flame cells, *m*, a sense cell, terminating below the cuticle above, and connected below with the nerve plexus, *n*, a myoblast, *o*, the processes of myoblast terminating in the circular muscles, *p*, free end of sense cell, *q*, a pore in the cuticle, above the *Korbchenzelle*, *r*, a small part of the most superficial layer of cuticle.

the necks of gland cells or a nerve fibre. There can be no doubt that the "subcuticula," of which there have been various interpretations, as in the case of Trematodes, is a true epidermis, consisting of spindle-shaped cells which send fine processes upwards through the basement membrane, to cease at the cuticle. The epidermic cells form a continuous "epithelium" in *Triaenophorus*, but this continuous sheet is interrupted in *Ligula*, and still more in *Taenia* and the majority of Cestoidea, by intrusive parenchyma, which may also be accompanied by muscle fibres; indeed, in *Taenia* the thin layer of circular, and the longitudinal coat of the "dermal" musculature come to lie between the "subcuticula" and the basement membrane.

The bulk of the musculature, however, lies below the "subcuticula", the outer coat of the parenchymal musculature consists of longitudinal fibres, which in the young part of the chain (or throughout the worm in *Ligula*) are continuous from one proglottid to another, but as these become more and more deeply constricted, the muscular coat becomes interrupted, in the higher Cestodes this longitudinal coat is often separated by parenchyma into outer and inner layers. The inner muscular coat consists of a sheet of transverse fibres on the dorsal and on the ventral surfaces, discontinuous at the right and left margins, these transverse muscles are also, at first, continuous from joint to joint; they delimit a central or medullary part of the parenchyma from a cortical part. In the Cestoidea, as in the Trematoda, the same controversy has raged as to the character of the parenchymal tissue; the most recent investigations, and the use of the most modern methods, tend to show that the parenchyma consists of very greatly branched cells, the processes from which, nutritive in function, extend in all directions, and are extensively ramified (Blochmann). These cells lie in a homogeneous matrix, containing vacuoles filled with a coagulable fluid This ground substance, which is not cellular, as Leuckart and others believed, extends right up to the basement membrane, interrupting the continuity of the epidermic layer of cells. In this parenchyma, and chiefly in its cortical region, are the characteristic "calcareous corpuscles." Each is structurally very similar to a fat cell—that is, the concentrically marked spherical concretion of lime is enveloped in a protoplasmic membrane, the nucleus being on one side (Blochmann). These lime corpuscles consist of about 21 per cent of lime, the rest being organic substance; the lime is in the form of carbonate, partly of albuminate (Griesbach), and perhaps even of a certain amount of urate. Originally considered as an excretory product—and described as lying in the excretory canals, which they do not—they are now usually regarded as "skeletal" (Leuckart), or as counteracting the acidity of the gastric juices. However, they do not disappear with age; nor is it

likely that the gastric or other digestive juices can pass through the thick cuticle. The lime corpuscles are, moreover, present in Cysticerci, which cannot be affected by gastric juice. Monticelli has found a red pigment associated with the lime corpuscles in *Scolex polymorphus*.

The excretory system of the Merozoa (see Pintner, Fraipont) consists typically of a superficial (cortical) network of fine capillaries, into which the flame cells open, and a system of collecting vessels in the medullary region extending throughout the strobila and entering the "scolex." Of these collecting vessels there are normally two on each side—a dorsal and a ventral—situated near the margin of the proglottids. These canals are at first equal, but during growth generally become unequal in diameter, the dorsal being the smaller, resulting in a complete disappearance of this one in several *Taenia*, spp, and in some Tetraphyllidea[1] The two canals of one side pass into one another in the scolex, while at the hinder end of the strobila, *i.e.* on the last proglottid, they open into a contractile bladder, and so to the exterior. This is the condition in the larval form, but various modifications may occur in this type—modifications which have no systematic importance (Fig VI.). In *B. latus* there are the deep longitudinal canals, which have a normal, dorsal, and ventral position; and further, the dorsal canals occur only in the young proglottids, and the transverse canals are at irregular intervals But whereas this segmental anastomosis occurs in these Dibothridiata, and again in the *Taeniidae*, it is absent in most of the Tetraphyllidea The two canals of one side, however, always pass into one another in the scolex, but the transverse cephalic anastomosis may be absent even here, as in most of the Tetraphyllidea (Fig. VII.), in others it is represented by a simple transverse canal, as it is also in Tetrarhyncha, whilst in the *Taeniidae* its place is taken by a circular canal arising, according to Pintner, by the splitting of this, in connection with the formation of a retractile rostellum.

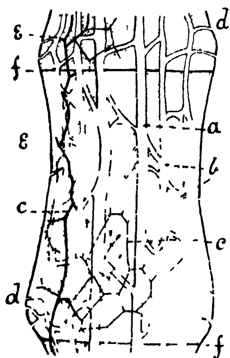


FIG VI

The excretory system in a proglottid of *Bothriocephalus punctatus*, v Ben (after Fraipont) *a*, the largest longitudinal canal (= ventral), connected to its fellow by several irregularly arranged commissural vessels, *b*, the two smaller, derived from the single dorsal canal of each side connected together by [illegible] anastomoses (Island formation of [illegible]), *c*, superficial network, represented only partially on the left side, from it the flame cells arise This network communicates with the dorsal canals at *e*, *d*, foramina secundaria (Wagener) iregularly arranged, *f*, limits of a proglottid

[1] Blochmann identifies Sommer's "plasmatic canal" as the dorsal excretory canal of *Taenia solium* and *T. saginta* (*Centralbl. f. Bakt v. Parasitenkunde*, xii. 1892, p. 373).

The posterior contractile bladder naturally persists only in those genera which do not drop their proglottids, *e.g.* *Ichthyotaenia*, and various *Taenia*, spp., which inhabit Teleostei; in other cases, after the separation of this terminal proglottid, the four collecting canals

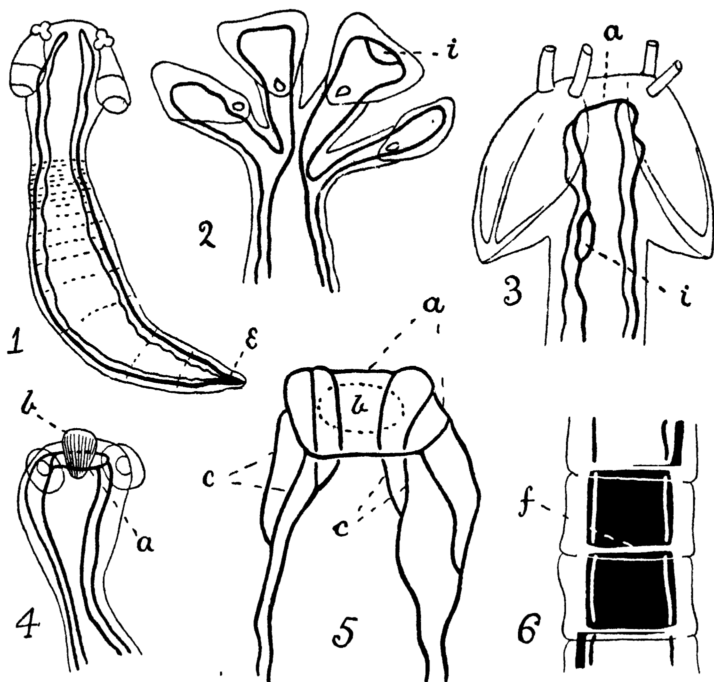


FIG VII —Plans of excretory system (after Pintner)

1 —*Acanthobothrium coronatum*, Rud Young The two canals on each side pass into one another in the scolex, but are not connected right and left Posteriorly all four open into the contractile bladder (*e*)

2 —*Phyllobothrium gracile*, Wedl Scolex The two canals of either side pass into the phyllidia of this side, *i* is an "island" formed by the local splitting of a canal and the reunion at once of the two branches

3 —*Tetrarhynchus* Scolex The frontal, transverse vessel (*a*) unites the right and left canals at the point of recurrence

4 —Scolex of *Cysticercus arionis* (*i e* of *Taenia multiformis*) *b*, rostellum, which causes the vessel (*a*) to form a circular loop, into which the four canals fall

5 —*Taenia* Scolex The muscular sucker also causes the formation of a loop in each of the longitudinal canals *a*, the circular vessel, *b*, position of the rostellum, *c*, the four acetabular loops or islands

6 —*Tetrarhynchus* and Tetracotylea Proglottids The ventral canal becomes wider than dorsal, and there is a transverse canal (*f*) in each proglottid

came to open independently; or, in some cases, a median duct develops from the last transverse connecting canal. But in a considerable number of instances the main canals effect new lateral communications in the scolex, neck, and proglottids; these "foramina secundaria" appear in *Schistocephalus* to be segmentally repeated.

The nervous system of *Bothriocephalus* (Fig. VIII.) consists of a right and a left longitudinal cord traversing the strobila throughout its length, lying nearer to the middle line than to the margin. In the scolex they are united by a "cerebral commissure," containing ganglion cells, whence four nerves pass back along each side of the scolex. The nervous system in the Merozoa generally agrees with this simple type; there is always one, sometimes two, marginal nerve cords, which are, in several instances at least amongst the higher forms, united by a transverse or circular commissure near the hinder margin of each proglottid (Tower (47), and others) A superficial network of nerve fibres is in connection with these main cords (Blochmann).

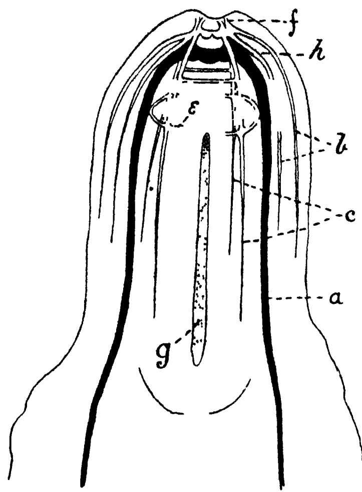


FIG VIII

Bothriocephalus latus, L Plan of the nervous system of the scolex (altered, from Niemec) *a*, one lateral nerve which extends throughout the entire strobila, *b*, the two lateral accessory nerves of one side, *c*, one dorsal and one ventral accessory nerve of one side, *e*, the incomplete circular commissure connecting the main nerve and the accessory nerves, *c*, *f*, the anterior nerves, *g*, one bothrium, *h*, the transverse ganglionic commissure (brain), in front of which is a small additional commissure

In the scolex the cords are always connected by a transverse cerebral commissure, and usually there are one or even two accessory, circular connections, whence more or less numerous nerves are given off (Fig. IX.). The degree of complexity of this apparatus is connected with the development and needs of the organs of the scolex, and appears to have no systematic value (Niemec, 31).

The most important of the internal organs from the systematist's point of view are the genital organs, these in *B latus* are fully developed in about the 600th proglottid, which is therefore said to be "mature." On the ventral surface of such a proglottid two pores lie in the median line; the anterior pore is the opening of the genital atrium into which open the male copulatory duct or penis, and the female copulatory duct or vagina, the posterior aperture is the "birth-pore" or opening of the uterus (Fig. III. 4).

In the youngest proglottids, immediately following the head, no trace of the genital organs occur, but as the proglottids grow older, and become further removed from their point of origin, the forecasts of the organs make their appearance, the male organs

first, and further back the female system. As the proglottids become mature they drop off in groups. The follicular testes are scattered over the greater part of the dorsal surface (Fig. X.); the numerous efferent canals unite to form a larger sperm-duct, which, after an extremely undulating course, enters and traverses the "cirrus pouch," to the muscular walls of which the duct is connected by radiating reticular fibres. By the contraction of the wall of the pouch, the sperm-duct is straightened out and the whole cirrus is everted. The germarium is made up of a pair of groups of acini, lying near the ventral surface, and it is noteworthy that, while in the Trematoda the testis is posterior to the germarium, the reverse

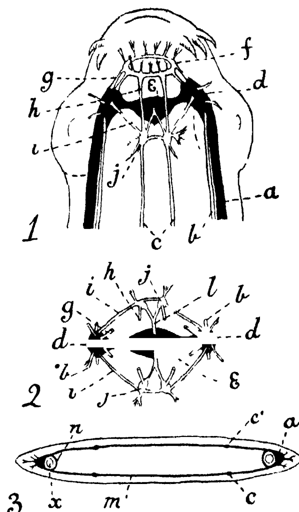


FIG IX

1, 2—Plan of the nervous system of the scolex of *Taenia* (reconstructed from Niemec's figures)

1—View from the ventral (or dorsal) surface *a*, lateral nerve, *b*, one of the two accessory lateral nerves, *c*, the ventral (or dorsal) nerves, *d*, the ganglionic enlargement of the lateral nerve, *e*, the transverse commissure, *f*, nerve ring round the rostellum giving off nerves forwards Posteriorly it receives eight nerves *g*, two nerves to the lateral ganglion; *h*, a pair of ventral (and dorsal) nerves, *i*, polygonal commissure, *j*, one of the two ventral (or dorsal) ganglia situated on this polygonal commissure, and connected to the main transverse commissure by the nerve (*l*)

2—Plan of nervous system at the level of the commissure, seen from above, after removal of the "ring"

3—Diagrammatic transverse section through the hinder margin of a proglottid of *Moniezia* (somewhat altered from Tower) *a*, lateral nerve, here dilated to form a ganglion, which is connected with its fellow by a ring-commissure, *m*, *c*', the dorsal and ventral ganglionic swellings at the junction of the dorsal and ventral nerves, with this commissure, *n*, a loop round the ventral excretory canal (*x*)

holds in the Cestoidea on the assumption that the scolex is anterior. The vitellarium consists of a vast number of follicles distributed over the ventral, and partially along the dorsal surface at each side. The uterus is a long tube, having a characteristic convoluted course, and opens anteriorly. The vagina starting from the ootype is straight (see 45).

The life-history of *Bothriocephalus* is incompletely known, though the development of the egg as far as the six-hooked embryo[1] has been carefully studied by Schauinsland (40) It is, on the whole, similar to that of a Trematode, in the character of its segmentation, at the end of which a "yolk envelope" of flat cells is formed, which is left behind in the egg-shell (Fig. XI.). Within this envelope

[1] The six-hooked embryo is also known as proscolex, onchosphere, and hexacanth embryo

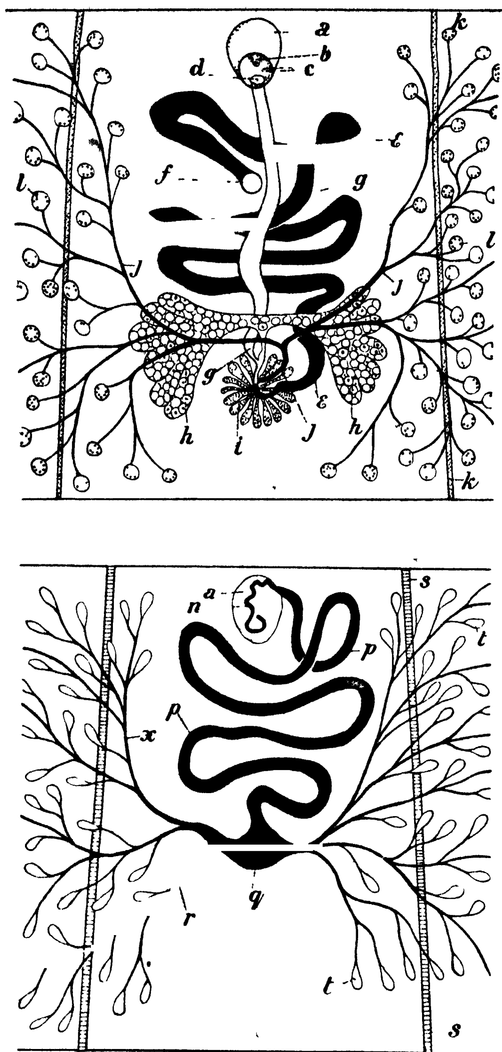


FIG X

Bothriocephalus latus, L. The genital organs (after Sommer and Landois) The upper figure shows the female organs seen from below, the lower figure, the male organs from above In each case only the central part of the proglottid is represented, so that only a small part of the testes and vitellaria is shown (see Fig III 4), the anterior and posterior boundaries, however, are shown *a*, the prominent "cirrus sac", *b*, the cirrus, partly everted, carrying the aperture of the sperm duct at its end, *c*, the genital atrium and pore, *d*, the vaginal pore opening into the atrium, *e*, the large coiling uterus; *f*, the uterine pore, *g*, the vagina in the middle line, *h*, germarium, *i*, shell gland, *j*, vitello duct, *k*, lateral nerve, *l*, vitellarium, *n*, cirrus canal traversing the muscular tissue of the cirrus sac in order to reach the male pore (see upper figure), *p*, sperm duct; *q*, seminal vesicle, *r* and *x*, vasa efferentia, *s*, lateral excretory canal, *t*, testicular follicles.

there is developed from the superficial blastomeres of the embryo a ciliated mantle or "embryophore" enclosing the solid six-hooked embryo, which is developed from the central mass of blastomeres.

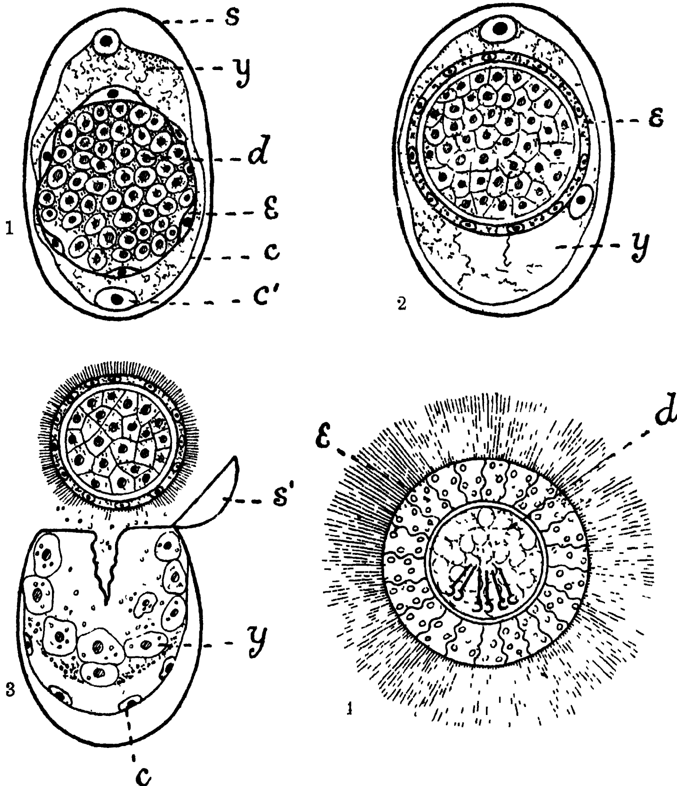


FIG XI —Development of *Bothriocephalus latus*, L (after Schauinsland)

1 —Segmentation is completed, some cells of the blastosphere have migrated through the yolk, and have flattened out to form (*c*) a "yolk envelope" A second set of superficial cells of the embryo have grown over the remainder, and have formed a layer (*e*) of flattened cells, the embryophore (Schauinsland's "ectoblast") The remainder (*d*) of the blastosphere will develop into the six-hooked embryo

2 —A later stage in which the embryophore (*e*) is becoming thicker

3 —The larva has been artificially pressed out of the shell, the operculum (*s'*) being pushed off The embryophore has developed cilia The yolk envelope remains in the egg shell, and now the yolk (*y*) is seen to consist of separate cells

4 —A free-swimming larva The embryophore (*e*) is much swollen by the water The six hooks are developed

This embryo leaves the thick operculated shell, still enclosed in the embryophore in *B. latus*, though in other species it is not ciliated and is left behind; by means of it the onchosphere is enabled to swim freely in the water for at least a week, rotating about an axis that

passes through one pair of hooklets, which is always carried hindmost. The fate of this onchosphere is unknown, as feeding experiments with appropriate hosts have been unsuccessful. But if we may judge from other histories, this embryo is swallowed by some invertebrate or perhaps a small fish on which the pike preys, for the tissues of this fish sometimes contain numerous encysted young forms of *Bothriocephalus*—wormlike, with an invaginable "scolex" or head at one end (Fig XII.). Such a sexless, encysted stage is known as a "metacestode" or "plerocestoid" (Braun). It is by eating such infested fish that man becomes the final host, in the Baltic provinces and elsewhere, where the pike is a favourite diet, and is eaten in an imperfectly cooked condition



FIG XII

Metacestode of *Bothriocephalus* encysted in the smelt (after Leuckart)

We have, however, more definite information about the history of *Ligula* and *Schistocephalus*, the ciliated larva of these worms is swallowed by a fish, and the six-hooked embryo makes its way through the intestinal wall, by the action of its hooklets, and thus reaches the body cavity. Here it develops directly, by growth and loss of hooklets, into the strobila, and in the case of *Schistocephalus*, the body even becomes segmented, indeed, the parasite only differs from the adult condition in the imperfect development of the genital organs. The great increase in size of the worm causes considerable inconvenience to the fish. When the latter is devoured by a bird, the tapeworm soon becomes mature in the intestine, the warmth of the bird's body hastening the development of the genitals. According to Leuckart, the strobila, after two and a half days' sojourn in the final host, may leave it through the anus, partially digested, it is true, and the eggs are thus scattered in the water.

The meaning of the ciliated embryophore is variously interpreted as either (*a*) a primitive ectoderm, or (*b*) the remains of a miracidium-like larva. The latter view commends itself at the present day, and the free-swimming larva may be compared to that of a Trematode, in which the "six-hooked embryo" may be regarded as having developed simultaneously with its envelope (cf. *Gyrodactylus*, p. 53).

CLASSIFICATION OF THE CESTOIDEA MEROZOA.

In the Merozoa the generative organs, more especially the uterus, exhibit two well-marked types of structure. In the one type, as in the Monozoa and *Bothriocephalus*, the uterus retains its

communication with the exterior by a "birth-pore." In the second type, this pore has been lost, so that the uterus is a closed sac (Fig. XIII.). In the former case, the eggs when ripe can pass out from time to time without a necessary separation of the proglottids; whereas, in the second case, the ripe proglottids drop off from the strobila, either singly or in groups, and the eggs are discharged only by local dehiscence or decay of its walls.

Associated with the possession of a birth-pore is the existence of only two adhesive organs of the scolex, whereas those Cestodes without a birth-pore possess four such organs, except in a few individual instances, where there is then evidence of fusion. These characters serve to differentiate the grade Merozoa into two branches—the *Dibothridiata* and the *Tetrabothridiata*.

These "organs of the scolex," comprehensively grouped as "suckers," occur in the Merozoa under three well-marked forms:

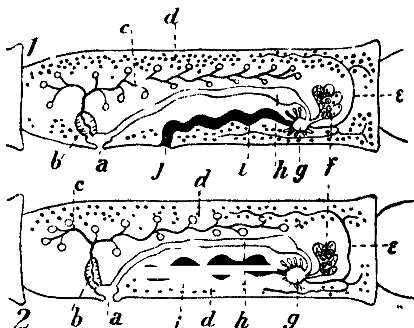


FIG XIII—Diagrammatic longitudinal median sections (or rather projections) of a proglottid.

1 Dibothridiata 2 Tetrabothridiata, showing the uterine pore in the former, its absence in the latter *a*, common genital (copulatory) pore, *b*, cirrus, *c*, vas deferens and testes, *d*, vitellaria, *e*, vitello-duct, *f*, germarium, *g*, ootype surrounded by shell glands, *h*, vagina (with dilatation or spermatheca) opening into the genital atrium, *i*, the uterus opening externally at *j*, in the Dibothridiata, but a blind sac in the Tetrabothridiata

(*a*) as sucking grooves or "bothria," which are narrow fissures or widely open cuppings on the dorsal and ventral surfaces of the head; their muscles are only slightly developed, and are not delimited internally from the parenchyma; they are characteristic of the Dibothridiata, (*b*) as "phyllidia" (or "bothridia," M. Braun[1]), which are essentially outgrowths from the side of the scolex, to the number of four. Each is more or less distinctly concave distally, this muscular cup is the "bothridium," the margins of which, and indeed the entire structures, are extremely mobile, and Pintner has suggested that these are rather organs of locomotion than of attachment. They present certain modifications (see below), and are characteristic of the Tetraphyllidea, Diphyllidea, and Tetrarhyncha. Finally, (*c*) as "acetabula," or suckers in the

[1] Van Beneden used the term "bothridium" for all kinds of sucking organs in the Cestoidea. Earlier writers used "bothrium." Braun uses "bothridia" for those which are here termed "phyllidia," and I restrict the use of the term to the cup or sucker carried by the phyllidium.

ordinary sense of the word. These are deep hemispherical cups or excavations at the side of the scolex, without projecting lips. They are not mobile, and their muscles are delimited internally. They are characteristic of the Tetracotylea (*Taeniidae*).

BRANCH A. DIBOTHRIDIATA

Cestoidea Merozoa, in which the scolex is provided with only two of these organs or "bothria," situated respectively on the dorsal and ventral aspect. The uterus retains its communication with the exterior

ORDER 1. **Pseudophyllidea**, v. Ben (**Dibothridae**, Dies.; **Dicestoda**, Perr.)

The scolex is usually unarmed, though hooklets occur in some genera. The common copulatory pore is usually on the ventral surface, though in a few forms it may move to the margin of the proglottid The uterine pore is ventral.

FAMILY 1. BOTHRIOCEPHALIDAE Bothria more or less definite slit-like furrows; proglottids generally distinct, and drop off in groups *Bothriocephalus*, Rud.; *B latus*, Bremser, in the intestine of man, in Russia, Switzerland, Southern France, North America. The embryos, enclosed in a ciliated embryophore, swim freely in water. Pike and other fresh-water fish are the intermediate hosts, but possibly they become infected by devouring invertebrates containing the larvae *B cordatus*, Lkt., in dog, Greenland *B tetrapterus*, v. Sieb, in *Phoca*. *B* (*Diplogonoporus*, Lonnb) *balaenopterae*, Lonnb, with two copulatory pores in each proglottid *B.* (*Krabbea*, R Bl) *grandis*, Bl, Japan *B* (*Anchistrocephalus*, Montic) *microcephalus*, Rud, in *Orthagoriscus mola* *Amphitretus*, R. Bl *B.* (*Diphyllobothrium*, Cobb) *stemmacephalum*, Cobb., in Porpoise *Amphicotyle*, Dies, with an accessory sucker to each bothrium *Bothriotaenia*, Railliet, they occur mostly in fish *B infundibuliformis*, Rud, in the salmon (Fig III 2), (see 38) *B rugosa*, Rud, lives in *Gadus*, spp (="*Abothrium gadi*" of van Beneden) *Disymphytobothrium*, Dies, with peculiarly modified head, in North American sturgeon *Schistocephalus*, Crepl. (see 17) *S solidus*, Crepl, in aquatic birds, the young form lives in the body cavity of *Gasterosteus*, in which it develops so far as to become segmented; the genital organs have already appeared. *Ligula*, Bloch, body unsegmented externally; final host is some aquatic bird; the intermediate host a Cyprinoid or other fish, in the coelom of which the worm attains considerable development (see 8) *L monogramma*, Crepl., a single series of genitals *L digramma*, Crepl, two alternating series FAMILY 2 SOLENOPHORIDAE The lips of each bothrium meet to form a sucking tube, usually retaining a pore at each end; genital pores ventral. *Solenophorus*, Crepl (*Bothridium*, Blv.), (see 7); *S. megalocephalus*, Crepl, intestine of boa and python (Fig III 3). *Duthiersia*, Perr.; *D. expansa*, Perr, intestine of *Varanus* (Fig III 6); *Diplocotyle*, Kr., *D obrikii*, Kr, in *Salmo carpio*, *Ptychobothrium*, Lonnberg, *P. belones*, Lonnb. FAMILY 3. BOTHRIOMONIDAE The two bothria are replaced by a terminal, unpaired cup, which has arisen either by

fusion and modification of the bothria, or it may be a rostellar sucker. *Cyathocephalus*, Kessl.; *C truncatus*, Pall., in fresh-water fish (Fig. XIV.), (see 19). FAMILY 4. LEUCKARTIIDAE. Without apparent bothria. *Leuckartia*, Moniez, in fish; *Blanchardella*, Moniez. FAMILY 5. TRIAENOPHORIDAE. Body indistinctly segmented, copulatory pore marginal. The bothria are very shallow, but wide; each is armed distally with two three-pronged hooklets. *Triaenophorus*, Rud.; *T. nodulosus*, Rud., in pike, and encysted in the tissues of Cyprinoid fishes (Fig XV.).

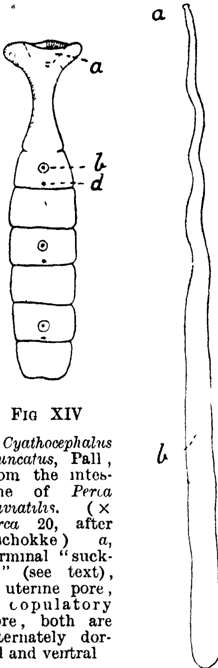


FIG XIV

Cyathocephalus truncatus, Pall, from the intestine of *Perca fluviatilis*. (× *circa* 20, after Zschokke) *a*, terminal "sucker" (see text), *b*, uterine pore, *d*, copulatory pore, both are alternately dorsal and ventral

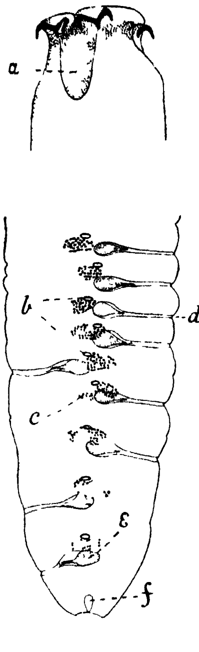


FIG XV.

FIG. XV.

Triaenophorus nodulosus, Rud, from the intestine of the pike The left-hand figure represents the entire strobila (× 2, orig) *a*, the scolex, *b*, the series of uterine pores which alone mark the repetition of parts, for there are no distinct proglottids

The right-hand upper figure is the scolex (× 17, orig) It is viewed rather obliquely, so that a part of one of the hooks of the dorsal surface is shown in addition to the bothrium (*a*) and the two characteristic hooks of the ventral surface

Lower figure The hinder end of the strobila rendered transparent (× *circa* 20, orig) *b*, uterine pores, *c*, uteri filled with eggs, *d*, copulatory pores, irregularly arranged right and left, *e*, cirrus, *f*, excretory bladder The rest of the genital organs not presenting any peculiarities are omitted

Further Remarks on the Dibothridiata.—This branch of the Merozoa is more nearly allied to the Monozoa than are the Tetrabothridiata. The majority of them are parasitic in fresh-water fishes, though the genus *Bothriotaenia* occurs in birds, and *Bothriocephalus latus* in man. The size of the strobila and the number of proglottids varies considerably, as it does too in the other orders; the great *Bothriocephalus latus*, with its hundreds of proglottids, and measuring some 20 feet or more, contrasts with *Cyathocephalus*, with only some twenty segments, and a length of 20 mm.

The scolex, though always retaining the two bothria—one dorsal, the other ventral—exhibits some interesting modifications of the typical structure. The deep, narrow cleft of *Bothriocephalus* is repre-

sented by a slight pit in *Ligula*, and in *Triaenophorus* by a wide, shallow depression. An accessory sucker, such as frequently occurs in the Tetraphyllidea, is met with in *Amphicotyle*, above the limits of the bothria. An extension of the bothria round the scolex, and their fusion, may lead to the condition in *Cyathocephalus*, where a circular disc is formed, capping or surrounding the scolex. Modification in another direction, viz. by the union and coalescence of the lateral lips of the bothrium, leads to the formation of a dorsal and a ventral tube, as in the Solenophoridae; by the closure of the lower aperture in *Diplocotyle*, two "suckers" are simulated; and in *Duthiersia* the upper opening is expanded, and the whole sides much folded to form a very mobile organ recalling the "phyllidium" of the Tetraphyllidea Further, in a few cases, hooklets are carried by the scolex; these aid very materially in fixing the parasite to the wall of its host intestine The scolex may be prolonged beyond the bothria, to form a "rostellum," which in *Ptychobothrium* is long and mobile; and in *Schistocephalus* is provided with a small pit, recalling the terminal sucker of other orders. Indeed, as will be seen below, modifications and differences of the same character as these occur again and again in different orders of the Merozoa. The typical "proglottidisation" is not expressed externally in *Ligula* and *Triaenophorus*, though the genital pores indicate the repetition of the genital organs (Fig. XV), in other cases, also, the demarcation of the proglottids is but feebly expressed (*Cyathocephalus* and *Diplocotyle*).

The copulatory pore, though typically ventral, may move outwards so as to become marginal (Fig III. 5), and may even come to lie on the dorsal surface in *Ptychobothrium* But these differences in position seem scarcely sufficient, by themselves, to justify new genera, and far less new families, and it is a matter of speculation as to which is the more primitive position Throughout this order the penis opens into the genital atrium in front of the vagina, and as a rule the birth-pore is behind the copulatory pore, but the reverse holds in *Bothriotaenia*.

Branch B Tetrabothridiata.

Cestoidea Merozoa, in which the scolex is provided with four organs of adhesion (? or locomotion), and in which the uterus is a closed sac, so that the eggs can escape only after the decomposition or rupture of the proglottid.

The branch includes four orders (families of van Beneden) founded chiefly on the character of the organs of the scolex. Tetraphyllidea, Diphyllidea, Tetrarhyncha, Tetracotylea.

Order I. **Tetraphyllidea,** v. Ben. (= **Tetrabothridae,** Dies.).

Tetrabothridiate Cestoidea in which the organs of the scolex are outgrowths from it; these "phyllidia" are more or less, but always

slightly, cupped, their margins being extremely mobile and active. The phyllidia may be pedunculated, their depressions ("bothridia") may be subdivided by ridges into loculi, and in a few cases carry hooklets. The copulatory pore is usually marginal; the vagina is anterior to the penis. The proglottids are detached singly, even before the genital organs are fully developed.

The members of this order are found almost exclusively in the spiral intestine of Selachians (see v. Beneden, 2).

FAMILY 1. TETRABOTHRIDAE (*Tetraphyllidea*, v. Ben.) The phyllidia are distinctly constricted at the base SUB-FAMILY 1. TETRABOTHRINAE. Phyllidia simple and attached by a broad base. *Phyllobothrium*, v. Ben. (Fig. XVI. 3), *Tetrabothrium*, Olss; *Calyptrobothrium*, Montic.; *Monorygma*, Dies.; *Ceratobothrium*, Montic.; *Oryg matobothrium*, Dies.; *Marsipocephalus*, Wedl.; *M rectangulus*, Wedl., in *Heterobranchus anguillaris* of the Nile; *Prosthecocotyle*, Montic.; *P forsteri*, in dolphin; *Dinobothrium*, v. Ben.; *Diplobothrium*, v. Ben.; *Zygobothrium*, Dies.; *Pelichnibothrium*, Montic.; *Peltidocotyle*, Dies, scolex globular, dilated, with four "scutella" (? phyllidia), each with two accessory suckers. *P rugosa*, Dies, in *Platystoma tigrinum* from Brazil, *Ephedrocephalus*, Dies. Small tetragonal scolex, with phyllidia at the angles The short neck is dilated to form a flat, octagonal platform, with reflexed edges, from which the scolex arises; Brazil *Amphoteromorphus*, Dies.; *Amphoterocotyle*, Dies. SUB-FAMILY 2 PHYLLOBOTHRINAE, v. Ben Phyllidia unarmed, more or less complicated by subdivision into "loculi," each phyllidium attached by a narrow base, which is frequently produced to form a peduncle *Echeneibothrium*, v Ben (Fig XVI. 4); *Rhinebothrium*, Lint (Fig XVI 2); *Spongiobothrium*, Lint; *Anthobothrium*, v. Ben. (Fig. XVI. 1), *Crossobothrium*, Lint, *Anthocephalum*, Lint SUB-FAMILY 3 PHYLLACANTHINAE, v Ben Phyllidia armed with hooklets. *Calliobothrium*, v. Ben. (Fig XVII. 1); *C* (*Acanthobothrium*, v. Ben) *coronatum*, Rud; *C.* (*Onchobothrium*, Blv) *uncinatum*, Rud.; *C* (*Prosthecobothrium*, Dies) *dujardini*, Dies, *Phoreiobothrium*, Lint; *Cylindrophorus*, Dies.; *Thysanocephalum*, Lint (Fig. XVII. 2), *Platybothrium*, Lint.; *Pelyonchobothrium*, Dies.; *P septicolle*, Dies, in *Polypterus bichir*. FAMILY 2. GAMOBOTHRIDAE, Lint The four phyllidia united by their lateral margins to form a single discoid or globular mass *Lecanicephalum*, Lint (Fig. XVII 3, 4). *Tylocephalum*, Lint, head formed of a globular organ (? united phyllidia) with four accessory suckers, and beyond a large rostellum. *T. pingue*, Lint, in *Rhinopterus*, *Discocephalum*, Lint. (Fig. XVII. 5).

Remarks on the Tetraphyllidea.—The anatomy, as well as much of what is known of the life-history of these forms, was investigated by van Beneden, to whose valuable researches we owe so much of our knowledge of parasitic Platyhelminths. These Tetraphyllidea are almost exclusively found in the spiral intestine of Selachians, and it appears that here they move about and are not permanently attached as the more highly developed *Taeniae* are; this locomotion is effected partly, at least, by the movement of the "phyllidia."

These "phyllidia" are outgrowths of the scolex, and contain a part of the excretory network (Fig. VII. 2); they occur under three chief varieties: (*d*) They retain their simple character with a more or less marked, spoon-shaped depression or "bothridium"

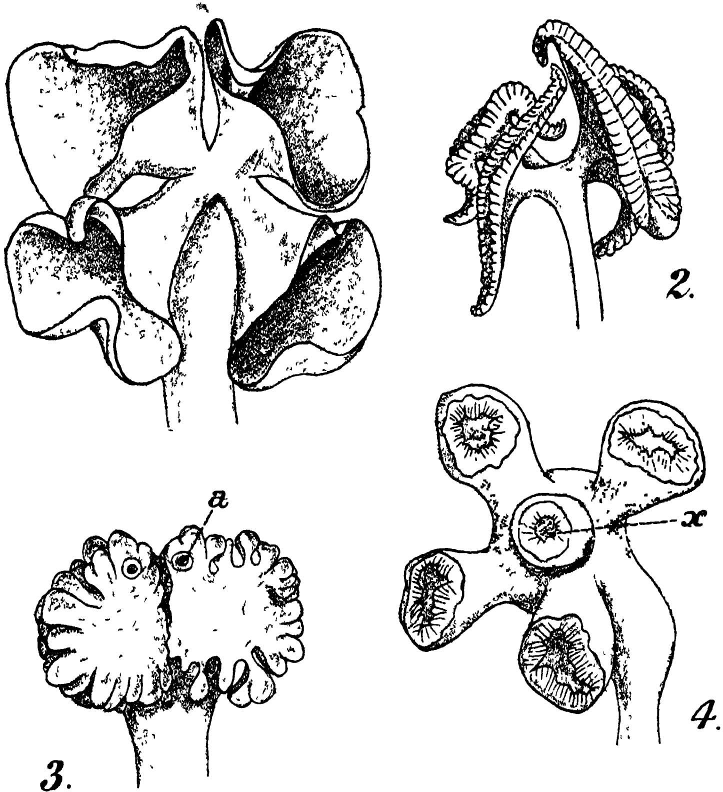


FIG. XVI.—Scolex of various Tetraphyllidea.

1.—*Anthobothrium cornucopia*, v. Ben., out of *Galeus canis* (after v. Ben.). The four phyllidia are typically developed, with long stalks, and a simple unarmed and undivided bothridium.
2.—*Rhinebothrium flexile*, Lint., out of *Trygon centrura* (after Linton). Each bothridium is divided into numerous loculi by a median, longitudinal, and a series of transverse ridges.
3.—*Phyllobothrium thridax*, v. Ben., out of *Squatina vulgaris* (after Zschokke). Each bothridium is provided with an accessory sucker (*a*).
4.—*Echeneibothrium variabile*, v. Ben., in various species of *Raia* (after Linton). In addition to the usual four bothridia—here well developed—carried by the phyllidia, there is an apical, rostellar sucker (*x*).

at the free end; the point of attachment to the scolex is constricted, and this narrow base may be prolonged to form a distinct peduncle, or this simple depression in the *Phyllobothrinae* (Fig. XVI. 2) may be subdivided by transverse ridges into a small number of "loculi," as in the posterior sucker of such a Trematode

as *Tristomum* or *Aspidogaster*. This loculation no doubt aids in attachment. (*b*) In the sub-family *Phyllacanthinae*, (Fig. XVII. 1) hooklets may be added which convert the originally locomotor organ into a more useful adhesive organ. (*c*) But both in the simple and in the armed phyllidia an "accessory sucker" may be present, either somewhere within the area of the cup (*Tetrabothrium*), or frequently above it (*Phyllobothrium*) on the scolex; this accessory

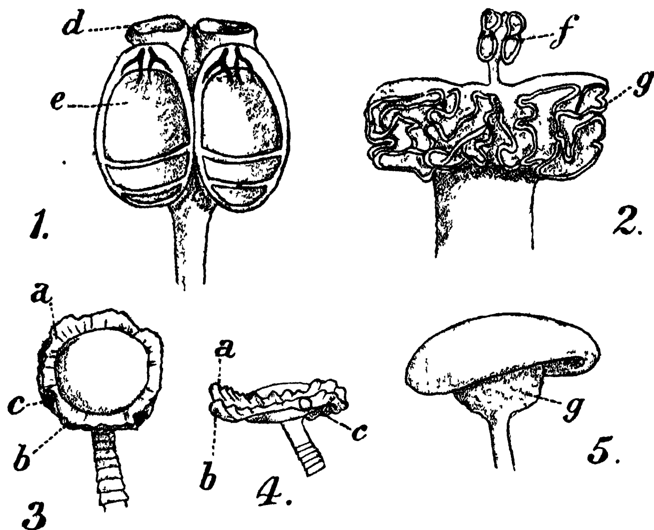


FIG. XVII —Scolex of various Tetraphyllidea

1 —*Calliobothrium filicolle*, Zsch, out of *Torpedo ocellata* (after Zschokke) The phyllidia are here short, each bothridium is trilocular, and is armed, distally, with two bifurcate hooks Above each bothridium (*e*) is an accessory sucker (*d*)

2 —*Thysanocephalum crispum*, Lint, out of *Galeocerdo tigrinus* (after Linton). The small scolex (*f*) is, during life, partially concealed by the "pseudoscolex" (*g*), which is formed by the development of much-folded ridges from the neck. Each bothridium (*f*) is bilocular, and armed with two simple spines

3 *Discocephalum peltatum*, Lint, out of *Trygon centrura* (after Linton) Viewed from above

4 The same from the side The scolex is here flattened so as to form two horizontal plates, the margins of which (*a*, *b*) are membranous and folded, and separated by a slight furrow. The lower plate carries four accessory suckers (*c*), two of which are indicated by the dark spots in 3, and one in 4, in which, however, the index line stops short

5 —*Discocephalum pileatum*, Lint, out of *Carcharius obscurus* (after Linton) The scolex is a flattened, mushroom-shaped disc, below it is a swollen neck (*g*), the surface of which is irregular, it is separated by a groove from the scolex

sucker differs in structure from the "bothridium"; it is a pit in the surface, with strong muscular walls, which are delimited from the parenchyma; in fact, these "suckers" have the structure of the "acetabula" of the Tetracotylea, with which Pintner (1896) homologises them, regarding the "bothridium" as something not represented in the majority of the Tetracotylea.

But in addition to forms, in which the four organs are distinctly separate, there are other forms in which the structure of the head

is more or less modified by fusion of the phyllidia. In *Dinobothrium* the phyllidia are arranged in two pairs, the members of a pair being close together. In *Diplobothrium*, *Zygobothrium*, and *Platybothrium* the paired members are actually united, so that the head appears to possess only two instead of four phyllidia; but evidence of fusion is provided by the existence of a slight ridge traversing each apparent phyllidium. A step further, and the four phyllidia may fuse to form a single structure, as in *Gamobothridae*, giving rise to a plate-like or globular termination to the head (Fig. XVII. 3, 4).

In *Thysanocephalum* (see 25) the scolex is hidden by a great swelling of the neck, which becomes folded and fringed so as to give rise to a structure recalling the mobile organ of *Gyrocotyle*, much exaggerated (Fig. XVII. 2). Here the "neck" is replacing, functionally, the scolex, which is greatly reduced, and suggests that possibly in "*Phyllobothrium lactuca*," v. Ben., something of the same sort has occurred

The "rostellum" or apical region beyond the attachment of the phyllidia may or may not be present, it undergoes great modifications in some cases, and possibly in the *Gamobothridae* this organ shares in the formation of the very peculiar "head" (see 25) It may carry a terminal sucker (*Echeneibothrium*, Fig. XVI. 4), as in some of the Tetracotylea.

The four phyllidia or other organs of the scolex in the Tetrabothridiata are normally arranged at equal distances around the apex of the scolex, in such a way that, as the nervous and excretory systems show, two correspond to the dorsal and two to the ventral surfaces of the proglottids; in other words, each bothrium of *Bothriocephalus* is represented, topographically at least, by a pair of organs in the Tetrabothridiata It is not, however, probable that the latter organs are descended from such a Dibothridiate form by a process of duplication. We have no evidence from embryology that this process takes place; on the contrary, we have evidence that the reverse process obtains in some of the Tetrabothridiata. Nevertheless, the fact that, in the Dibothridiata, the generative organs resemble those of the Cestoidea Monozoa and Heterocotylea, forbids us taking the view that each of the two "bothria" in this branch has arisen by fusion of a pair of ancestral organs. We have, therefore, to fall back on the assumption that both groups have been derived, along divergent lines, from a common ancestor in which the organs of adhesion were not yet developed, or possibly were in some such condition as that of *Caryophyllaeus*.

The generative organs retain in some respects the arrangement found in the Dibothridiata, viz. the vitellarium is marginal and follicular, extending round the entire proglottid; the vagina is usually anterior to the penis; the uterus is more or less tubular and undulating, but has lost its pore. The genital pore is

marginal; but in *Ephedrocephalus* the male organ opens here, the vagina on the ventral surface. The eggs undergo little change so long as they remain in the uterus; but, as in the *Dibothridiata*, develop outside the parent, from which they are discharged by the decay of the joint. The proglottids are detached singly, and the fringe of processes or lobes which frequently ornament the hinder margin are used as locomotor organs, after separation the proglottid may grow, and the genital organs undergo further changes, so that there is a close resemblance to an "individual" organism leading its own independent life.

Very little is known about the life-history of the members of the order. Van Beneden discovered isolated heads attached to "sacs," or even enclosed in them, in various Selachians and other fishes, he noted the resemblance of these "scolices" to the heads of various Tetraphyllidea, and rightly concluded that they represent a stage in the life-history of the tapeworm Such "metacestodes" (which resemble Cysticercoids with everted head) occur free in the intestine of various fish, and no doubt attain their adult state when these are devoured as food by Selachians One of the commonest forms is *Scolex polymorphus*, which has been observed in a variety of Teleosteans, in *Sepia*, and even in crabs Monticelli (29) has shown, by careful comparison with the head of adult *Calliobothrium*, that it is the larva of *C. filicolle*, Zsch. In these metacestode stages the organism consists of a sac and a head, invaginable in some cases into the sac, the walls of which are thin, muscular, and provided with nerves and excretory canals, on the same plan as in the adult, the latter open by a contractile bladder posteriorly, and are continued into the scolex anteriorly. By a process of budding just behind the suckers, a series of segments are formed, and it appears that the orginal sac or bladder—upon which six hooks have in many cases been recognised—becomes the most posterior, sterile proglottid.

ORDER 2. **Diphyllidea**, v. Ben.

The scolex is provided with a long "head stalk," which is armed with several longitudinal rows of hooklets; the "head" consists of a retractile armed rostellum and four (apparently only two) phyllidia, with projecting, slightly mobile margins. The strobila consists of few proglottids The generative organs are of the Tetraphyllidian type, but the genital pore is on the ventral face.

SOLE FAMILY. ECHINOBOTHRIDAE. *Echinobothrium*, v. Ben, sole genus, in spiral gut of Selachians (Fig. XVIII.); *E. musteli*, Pintner, the metacestode in the liver of *Nassa reticulata*. The rostellum has an elaborate structure, consisting of a muscular mass lying dorsally and ventrally, supporting two groups of "frontal hooks." This rostellum appears to be homologous with that of the *Taeniidae* rather than with the proboscis

of *Tetrarhynchus* (33). Each of the two phyllidia, which are dorsal and ventral, consists really of two alae or flaps separated by the projecting edge of the scolex. These four flaps are indeed the four phyllidia, united

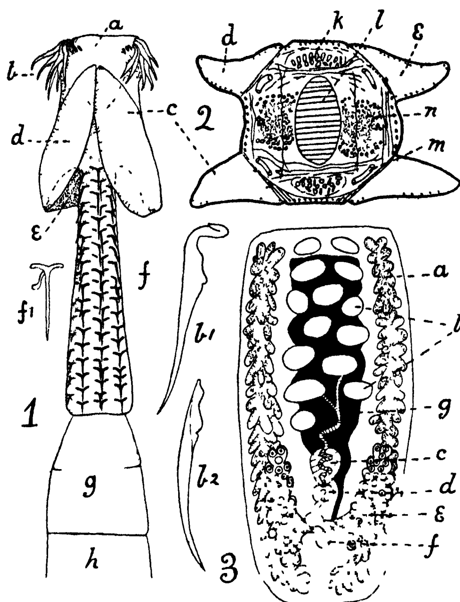


FIG XVIII

1.—*Echinobothrium affine*, Dies, out of *Raia*, spp (altered, after Pintner). View of scolex from the side, with the commencement of the body *a*, rostellum, *b*, rostellar or frontal hooklets, situated in a dorsal and ventral group of eleven, in each group there are two kinds—six like b^1, and five like b^2 in this species, at the sides of each group are three small accessory hooklets, b^1, b^2, the two kinds of frontal hooks of *E mustelı*, Pintner. The central muscular mass of the rostellum is indicated by dotted lines, but in addition there is a group of retractor muscles of the hooks on each side, *c*, one of the ventral phyllidia, *d*, *e*, the right and left dorsal phyllidia, united below, *e*, points to the inner face of the phyllidium, the dotted outline indicates the lower limit of these organs, *c*, *d*, are in reality separate from one another above, but are represented as overlapping, *f*, the long "head stalk" provided with eight rows of spines, characteristic of the genus In this species there are twenty to twenty-five spines in each row, f^1, one of these spines, it is quadriradiate, with its fourth spine directed inwards and slightly curved, *g*, the uppermost proglottid, which exhibits a notch at each side, indicating, probably, a division into two, *h*, the second proglottid

2—Transverse section of the scolex, a little above the level of *c*, in 1 (altered, after Pintner) The parenchyma of the four phyllidia is not indicated, the longitudinal muscles (as a row of dots) below the cuticle *c*, one of the ventral phyllidia, *d*, *e*, the two dorsal phyllidia corresponding to those in 1 It is now seen that *d* and *e* are in reality separate structures, the body wall intervening between them, where the letter *b* is placed The figure "2" lies in the lateral depressions between *c* and *d*, *k*, the retractor muscles of the dorsal frontal hooks, *l*, the central muscular mass of the rostellum, formed of transversely arranged fibrillae, *m*, the four excretory canals, *n*, the great lateral ganglia of the nervous system, below the rostellar mass they are connected by a transverse commissure

3—Plan of the genital organs from below (composed from Pintner's description and figure of *E musteli*) In reality the testes would have undergone degeneration before the uterus had attained the size represented *a*, Vitellarium; *b*, testes, *c*, cirrus, *d*, genital atrium, which opens on the ventral surface of the proglottid, *e*, germarium, *f*, vagina dilated in its course to form a receptaculum seminis, *g*, uterus.

dorsally and ventrally (Fig. XVIII. 2). It is a noteworthy fact that Pintner could find no calcareous corpuscles anywhere in the tissues of this tapeworm.

The systematic position of this isolated genus presents considerable difficulty; it is evident that it is Tetrabothridiate both from the structure of its suckers and from the absence of a distinct birth-pore. The fact that the margins of the bothridia project freely and are slightly mobile points to its affinity with the Tetraphyllidea rather than with the *Taeniidae* or Tetrarhyncha, as also do the genital organs Its long "head stalk" is a point of resemblance to the latter group. This region is not one of budding as is a "neck" in the rest of the Merozoa, for there is a sharp demarcation between the region of budding and the armed region both in *Echinobothrium* and the region which contains the proboscis sacs in *Tetrarhynchus*. The fact that in both families there is a tendency for the bothridia to fuse in couples must not be held to have great weight, since in the Tetraphyllidea we find the same tendency in various genera The ventral genital pore too is not unknown amongst the Tetrarhyncha nor the Tetracotylea, but at first recalls the Bothriocephalid arrangement.

Probably *Echinobothrium* came off from the Tetrabothridiate stem at a very early period, and has remained thus isolated.

The genus *Tetracampos*, Wedl., may possibly be allied to *Echinobothrium*. The scolex possesses four round, flat, feebly expressed phyllidia; the rostellum carries four groups of hooklets, but nothing is said as to its retractility. The genital pores are on the ventral surface The hexacanth embryo is ciliated. *T. ciliotheca*, Wedl., in *Heterobranchus anguillaris* of the Nile (*Stzber Akad Wien Math. Nat* Cl I. xliv 1861, p 473).

ORDER 3. **Tetrarhyncha**, v. Ben. (= **Phyllorhyncha**, v Ben , = **Trypanorhyncha**, Dies).

The four phyllidia (bothridia) may be united in pairs, as in the *Diphyllidea* Each phyllidium is accompanied by a long spiniferous proboscis (or "trypanorhynchus," Dies) capable of retraction into a sac occupying the "head stalk." The adults occur in Selachians. The metacestode is encysted in various parts of Teleosteans FAMILY—TETRARHYNCHIDAE (= *Dibothriorhyncha* + *Tetrabothriorhyncha*, Dies, etc), with characters of the order. *Syndesmobothrium*, Dies , *Tetrarhynchus*, Rud. (= *Rhynchobothrium*, v. Ben., Lkt, etc) The genus contains a large number of species *T. ruficollis*, Eysenh., in *Mustelus*, *Acanthias*, etc , its metacestode is *Coenomorphus joyeuxii*, Lonnb, which occurs in crabs (Vaullegeard, 1895) *Rhynchobothrium*, Rud. (incl. var spp of *Tetrarhynchus*, auct); *Otobothrium*, Lint ; *O crenaticolle*, Lint, from *Zygaena malleus*

Remarks on the Tetrarhyncha.—The numerous species occurring in sharks have been, by various authors, referred to a variety of genera distributed over two families founded on the character of the bothridia,—whether they are two or four, independent or united. Pintner in a recent work (34) would refer all species to one genus *Tetrarhynchus*, for, as he points out, there is every gradation between the various conditions of the phyllidia.

The scolex in this group is extremely elongated, and, as in the Diphyllidea, is provided with a very long "head stalk," which is

distinctly and markedly constricted from the "neck" (Fig. XIX.). The head stalk carries the "head," which is nearly square; the

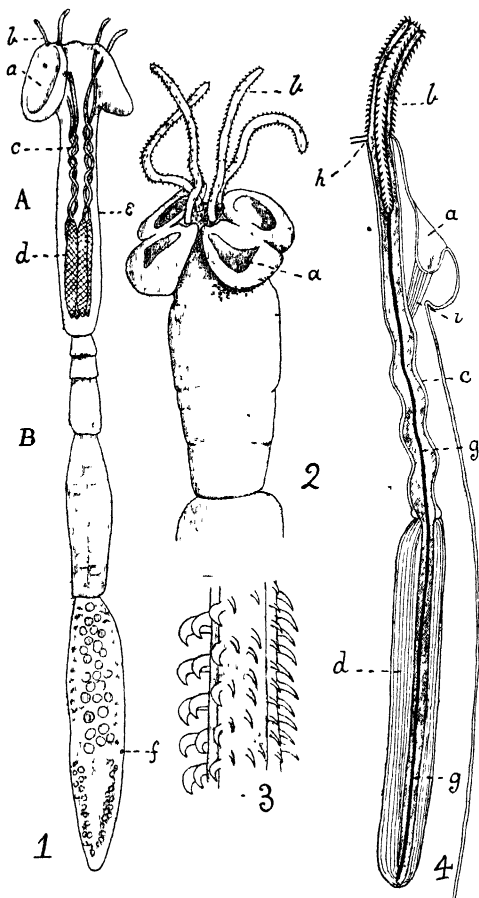


FIG. XIX

1.—[illegible] Lint., out of [illegible]. Entire strobila (× [illegible], after Linton) [illegible]. *B*, the "body [illegible] of five proglottids, the last of which is nearly mature. *a*, one of the two phyllidia, formed by the fusion of a pair; it bears a single bothridium; *b*, one of the four spiniferous proboscides; *c*, the membranous proboscis sheath; *d*, the muscular bulb; *e*, the "head stalk"; *f*, genital pore.

2.—*T.* (*Syndesmobothrium*) *gracilis*, Wagn., out of a cyst in *Orthagoriscus mola* (× 4½, orig., from a specimen in the Oxford University Museum). The scolex had not separated from the "bladder," a small portion of which is represented. *a*, one of the four independent and distinct bothridia; *b*, one of the four proboscides.

3.—A portion of a proboscis of *Tetrarhynchus*, sp., out of the intestine of *Carcharias* (× 90, orig.). The two kinds of hooks and their spiral arrangement are shown.

4.—Diagrammatic longitudinal section of a quadrant of a scolex, showing one bothridium, and one proboscis which is partially everted. *a*, Bothridium; *b*, proboscis; *c*, proboscis sheath, its cavity is shaded; *d*, muscular bulb, with its cavity shaded; *g*, retractor muscle; *h*, the aperture in the scolex, through which the proboscis is everted, and to the margin of which the membranous sheath is attached; *i*, retractor muscles of the bothridium, inserted in the proboscis sheath.

four phyllidia—set in dorsal and ventral pairs—may be distinct, terminal, and almost cup-shaped (*Syndesmobothrium*), but more generally the pair of organs are adnate (*Tetrarhynchus*), or even more or less closely united (*Otobothrium*), but there is frequently a ridge, or other sign of fusion However, in some cases this fusion is so complete externally that there appears to be only two phyllidia, as in Diphyllidea, but even then, the four structures are distinctly recognisable in section by the distribution of the nerves and excretory organs (*Rhynchobothrium*).

The characteristic structures of the order, however, are the four "proboscides" or trypanorhynchi (Fig XIX. 4).

Each proboscis consists of three parts (1) a longer or shorter hollow tentacle, capable of eversion and introversion, and armed with numerous hooklets arranged in a définite way. This tentacle can be withdrawn into (2) the tubular "membranous sheath," which starts from the apex of the head where it opens and passes backwards into the head stalk, taking a straight or undulating course; it terminates in (3) the "muscular bulk" or cylinder, the walls of which are formed of ten or more concentric sheaths of muscle fibres, which are transversely striated. The whole apparatus is filled with a fluid, by the compression of which in the "bulb" the tentacle is evaginated Introversion is effected by a "retractor muscle" attached at one end to the wall of the bulb, at the other to the tip of the tentacle The apparatus presents certain interesting histological features, for instance, the sheath is lined by a distinct epithelium Each individual proboscis resembles in some degree the single proboscis of *Acanthocephala*, in a less degree that of Nemertines. It has been usual to homologise these "proboscides" of *Tetrarhynchus* with the retractile rostellum of certain *Taeniidae*, but apart from the difference in number, there are differences in structure which militate against this view. It appears more probable (Pintner) that each proboscis has been developed by the deepening and modification of an "accessory sucker" of some Tetraphyllidean, as its relation to the bothridia, and its mode of development, closely agree with these structures. Functionally, too, it is a perfection of the armature *plus* the accessory sucker of three forms, whilst there is no doubt that the "phyllidia" of the two orders are identical. As will be shown below, the "acetabula" of Tetracotylea are derived also from the "accessory sucker," so that the proboscis of *Tetrarhynchus* is homologous with the sucker of *Taenia*.

The excretory (Fig. VII. 3) and nervous systems, which present nothing of any systematic value, have been worked out by Lang, Pintner, etc. As to the generative organs, they are constructed on the plan of the Tetraphyllidea, with marginal vitellaria, etc.

The metacestode phase is a cysticercoid, the head with its apparatus being enclosed in a bladder similar to that of Tetraphyllidea; this occurs encysted in various tissues, especially the wall of the gut, of Teleosteans, or with everted head, free in the alimentary canal of sharks. The bladder may be a foot or more in length, as *T. elongatus*, *T. macrurus.* The adults of some species were observed by v. Beneden with this "bladder" attached at the end of the strobila.

The scolex may after eversion separate from the bladder, and in this condition has been found in *Sepia* (as *T. sepiae*).

The cysticercoid, with the enclosed scolex, was known as *Floriceps* (Cuv.), and as *Anthocephalus* (Rud.), and the term *Tetrarhynchus* was applied to the stage with everted scolex; van Beneden showed that these are merely stages in the life-history of the strobila known as *Rhynchobothrium.* It is still undecided amongst systematists which of these two last names should be used.

ORDER 4. **Tetracotylea,** Dies (= **Taeniidae,** auct)

Tetrabothridiate Merozoa, in which the organs of the scolex have the form of cup-shaped or hemispherical "acetabula" hollowed out in the sides of the scolex, and without projecting or mobile margins[1] Hooklets are rarely present in these acetabula. There is usually a rostellum, which may be armed with a crown of hooklets Members of the order are mostly parasitic in warm-blooded vertebrates FAMILY 1. ICHTHYOTAENIIDAE, Lonnberg The sucking organs are acetabulate, but the generative organs resemble those of the Tetraphyllidea.[2] *Ichthyotaenia*, Lonnb (= *Tetracotylus*, Montic); several species in fresh-water fish (see 10 and 37). *Corallobothrium*, Fritsch (Fig XXII 1) FAMILY 2. ECHINOCOTYLIDAE The acetabula are armed; rostellum with one or two circlets of hooklets: parasitic in birds *Echinocotyle*, Blanch, a single crown of hooklets, which are falciform *E rosseteri*, Blanch, in the duck, "metacestode" in *Cypris cinereus. Davainea*, Blanch and Raillet (Fig. XXII. 7); *D. proglottina*, Dav, with four proglottids; fowl and slugs *D. contorta*, Zsch, from *Manis pentadactyla. Cotugnia*, Diam, with two sets of genital organs in each proglottid. *Idiogenes*, Kr ; *Ophryocotyle*, Friis. FAMILY 3 TAENIIDAE. Scolex globular or pyriform, suckers unarmed; rostellum may or may not be armed; vagina elongated, posterior to the cirrus, mostly parasitic in mammals, larval stage a "cysticercus" or "cysticercoid" SUB-FAMILY 1. HYMENOLEPINAE (= *Cystoidea*, Lkt) Strobila of moderate or small size, scolex with one, two, or several circles of hooklets, eggs with transparent, multiple envelopes; larva, a cysticercoid in Arthropods and Mollusca *Dipylidium*, Lkt, rostellum armed with peculiar hooklets, like

[1] In some avian tapeworms living in *Apteryx* the lower margin projects slightly and may be mobile (Benham, *Q J M. Sc* xliii. 1900, p 83).

[2] The genus *Sciadocephalus*, Dies. (Fig XXII), is doubtfully placed here It is by some authorities put in the family Gamobothridae, among the Tetraphyllidea. The family Ichthyotaeniidae, in fact is possibly a member of the latter order.

rose-thorns (Fig. XXIV.); genital organs and apertures double in each proglottid (Fig. XXVI.). *D. caninum*, L. (= *T. cucumerina*, Bloch.; = *T. elliptica*, Batsch), in the ileum of dog; cysticercoid in *Trichodectes canis* and in *Pulex serraticeps*. The strobila is 100 to 250 mm. long; the scolex has four rows of hooklets; the worm occasionally occurs in man. The larva of *D. echinorhynchoides*, Sons., occurs in lizards. *Hymenolepis*, Weinl., the proglottids much broader than long, with the posterior angles projecting like saw-teeth; genital pores all on the left side: uterus transverse; eggs with three envelopes, far apart, the innermost having "horns" (Fig. XXVIII.). *H. nana*, v. Sieb., in the intestine of man, was originally discovered in an Abyssinian; it is now known also from Italy, England, United States, and the Argentine. It is about an inch in length; the rostellum bears a single row of hooklets; the larva is unknown. *H. murina*, Duj., in rat and mouse; the larvae occur in the villi of the intestine, and the adult in the lumen; there is here, therefore, no change of host; there is merely a migration from one organ or part of an organ to another. Grassi has suggested that these species are synonymous, but v Linstow (1895) has pointed out the various differences between them. *Drepanidotaenia*, Raillet, in the gut of birds, especially aquatic birds; cysticercoids in small Crustacea. *D. infundibuliformis*, Goeze, in pigeon and house-fly; *Dicranotaenia*, Raill., *D. coronula*, Duj., duck and *Cypris*, *Chapmania*, Montic. SUB-FAMILY 2 TAENIINAE (= *Cystotaenia*, Lkt.). Strobila usually of large size; scolex with two or three circles of hooklets; uterus median, with lateral caeca; genital pores, irregularly alternate; eggs with two envelopes; the outer thin and deciduous, the inner one thick, brownish, and immediately enveloping the six-hooked embryo. The genus *Taenia* has been subdivided into a number of sub-genera by Weinland: *Taenia*, L (s str), rostellum armed; larva a cysticercus. *T. solium*, Rud, intestine of man; *Cysticercus cellulosae* in muscle and viscera of pig, rarely in man, rat, dog, etc. (Fig. XX 3) Cosmopolitan wherever the pig is a common article of diet, and eaten in an imperfectly cooked condition. Scolex with two circles of hooklets; strobila 2 to 3 metres long, with 850 proglottids, the 450th having fully-formed genital organs. The uterus consists of a median sac, with eight to ten broad caeca, which bear irregular wide lobes. *T serrata*, Goeze, in small intestine of dog, wolf, etc, with *C. pisiformis* in the rabbit and hare; *T. marginata*, Batsch, in wolf, butcher's dog, etc., is the largest dog tapeworm, measuring 1·5 to 3 metres Its *C tenuicollis* infests the peritoneúm, liver, etc., of pig and ruminants *Taeniarhynchus*, Weinl., has neither rostellum nor hooklets; the larva is a cysticercus. *T. saginata*, Goeze (*T. mediocanellata*, Kuch), in the intestine of man; its *Cystic bovis* in the muscles of ox (Fig. XX). Originally from the East, now cosmopolitan, where imperfectly cooked beef is eaten freely. It measures 7 to 8 metres, and is the largest tapeworm in man; there are about 1200 proglottids, relatively broad, the genital organs being fully formed in the 600th; the worm appears to be the ταινίαι of the Greeks. *Cystotaenia*, Leuck, scolex with two circlets of hooklets; the larva is a "coenurus." *C. coenurus*, Kuch., in the ileum of the dog and wolf; *Coenurus cerebralis*, in the brain of sheep (or other domestic and wild herbivora), swells up to a great size,

destroying more or less of the brain, causing the disease known as "gid" or "staggers." *C. serialis*, Raill., of dog, with Coenurus in the connective

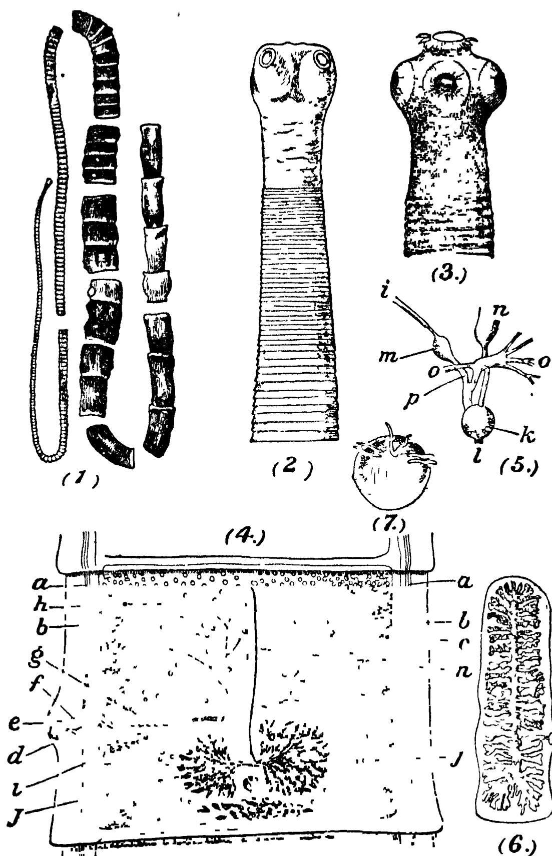


FIG XX

1 —*Taeniarhynchus saginata*, Goeze (× ½), entire strobila
2 —Anterior part of the same (× 8) as an example of unarmed tapeworms
3 —The scolex of *Taenia solium*, Rud (× 22), showing the rostellum with double crown of hooks.
4 —A genitally mature proglottid of *T saginata* (× 7) *a*, lateral nerve, *b*, lateral excretory canal, *c*, testes, *d*, genital papilla, *e*, genital pore, *f*, cirrus, *g*, sperm duct, *h*, testes, *i*, vagina, *j*, germarium The ootype and shell gland are unlettered The vitellarium is the small organ behind the germarium *n*, uterus
5 —The ootype and female ducts related to it (× 30) *i*, vagina, *k*, ootype, the shell glands not shown, *l*, vitello-duct, *m*, spermatheca, *n*, uterus, *oo*, germ ducts, *p*, fertilising canal, *i e* the lower end of the vagina
6 —A detached ripe proglottid of *T saginata* (× 2), with fully formed uterus filled with eggs
7.—Six-hooked embryo (All after Leuckart)

tissue of the wild rabbit and various rodents. *Echinococcifer*, Weinl., scolex with two circles of hooklets. The metacestode is known as

"echinococcus." *E. echinococcus*, v. Sieb., measure 5 mm., consists of only four proglottids, the last of which is ripe (Fig. XXI.). The strobila lives in the intestine of dog, wolf, jackal, in immense numbers. The "echinococcus" occurs in various tissue of ungulates, carnivora, rodents, monkeys, and may even find its way into man in countries such as Iceland and Victoria, where he and the dog are very closely associated, and where cleanliness is neglected; in the former country as many as two to three per cent of the inhabitants are affected. SUB-FAMILY 3. ANOPLOCEPHALINAE. Body lanceolate anteriorly; scolex unarmed and without a rostellum; proglottids being much broader than long, the uterus is transverse (Fig XXV.); the eggs contain a "pyriform apparatus" (see below). The adults occur in the intestine of ungulates. *Moniezia*, R. Blanch, two complete sets of generative organs and two genital pores in each proglottid. *M expansa*, Rud, in sheep (Fig. XXV 1). *Thysanosoma*, Dies, *T fimbriata*, Dies., in the small intestine and bile ducts of sheep, etc. *Stilesia*, Raill., suckers of the scolex directed forwards; in sheep *Ctenotaenia*, Raill, broad tapeworm of rodents. *Anoplocephala*, E. Blanch, scolex usually large (Fig XXII. 6); proglottids much imbricated; the proglottids are stated not to drop off, pyriform apparatus very well developed; in the *Equidae*. *Andrya*, Raill., in rodents. *Bertia*, R. Blanch.; *B studieri*, Bl, in chimpanzee. *Plagiotaenia*, Peters; *P. gigantea* in *Rhinoceros africanus*. *Amabilia*, Diam; *A lamelligera*, Diam, in flamingo FAMILY 4. MESOCESTOIDIDAE, Raillet. Head unarmed, with four terminal suckers; genital pores separate, on the ventral surface *Mesocestoides*, Vaill. (*Ptychophysa*, Hamann); *M. lineatus*, Goeze (= *T. lineata*, Goeze; = *T. litterata*, Batsch); in dog, cat, especially in Iceland The genital organs present some resemblance to those of the Tetraphyllidea; the uterus presents a single "ovarian capsule" (ovisac), the vaginal pore is anterior to the male pore, near the anterior end of the proglottid Ripe segments drop off separately. According to Neumann, the worm develops from "Dithridium" of dog, without an intermediate host

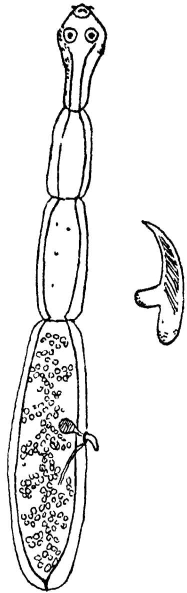


FIG XXI.
E echinococcus, v Sieb, out of the dog (after Perroncito). The strobila, and one of the rostellar hooklets

Remarks on the Tetracotylea.—This order contains those Cestodes which are parasitic in warm-blooded animals, as well as some few parasitic in Teleostean fish, and in Amphibia. Since all the human tapeworms, except *Bothriocephalus*, belong to it, the order has received more attention than the others, and it is customary to take one or other of the common species of *Taenia* (s. l) as a type of the whole class. For an account of the anatomy and mode of life of any human parasite reference should be made to Leuckart's

admirable text-book, while those infesting domestic animals are described in Raillet's *Traité de Zoologie, medicale et agricole.*

Certain fresh-water fish are inhabited by certain species of *Taenia* (s. l.), as well as by the genus *Ichthyotaenia*, and various species of anurous Amphibia by *T. dispar*. Birds are attacked by members of a special family, the *Echinocotylidae*, as well as by species of *Drepanidotaenia*, provided with a powerful armed rostellum, but the majority of species occur in Mammalia. Although in higher forms the parasite is confined to a single host, or to closely allied hosts, in

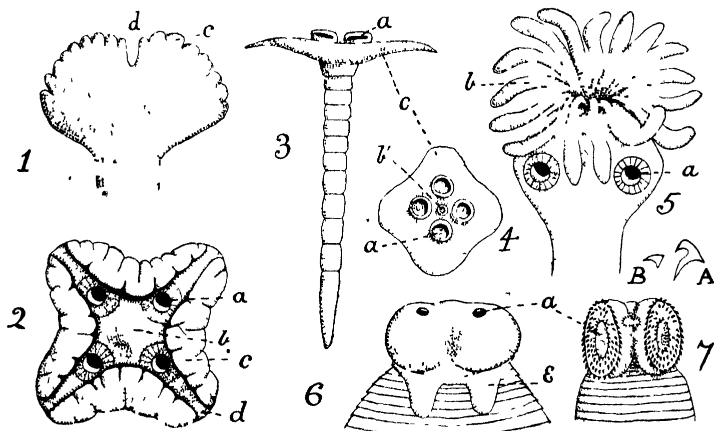


FIG XXII —Peculiar scolices of Tetracotylea *a*, acetabulum, *b*, rostellum, or its representative, *c*, expanded region

1, 2 —*Corallobothrium lobosum*, Rigg, out of *Pimelodus pati* (after Riggenbach), side view; and viewed from above (compiled from Riggenbach's descriptions and figures) *c*, the notched lobes rising up from below the scolex and hiding it, *d*, groove between them

3, 4 —*Sciadocephalus megalodiscus*, Dies, out of *Cichla monoculus* (after Diesing), side view and top view, *c*, disc-like expansion of the scolex

5 —*Parataenia medusia*, Lint, out of *Trygon centrura* (probably synonymous with *Polypocephalus*, Braun) *b*, the sixteen rostellar tentacles, capable of retraction, into a cavity in the scolex

6 —*Anoplocephala perfoliata*, Goeze, out of the caecum of horse (after Raillet) *e*, peculiar ear-like flap, regarded as homologous with the phyllidium of Tetraphyllidea

7.—*Davainea echinobothrida*, Mégn, out of *Gallus domesticus* (after Mégnin) The armed rostellum is indicated in a retracted condition *A*, rostellar hooklet, *B*, acetabular hooklet

those inhabiting fish, birds, the same parasite occurs in numerous hosts, and *vice versa*, one host contains numerous species of Cestodes.

In this order of Cestodes the organs of the scolex are true suckers (*acetabula*), the structure of which closely agrees with those of Distomid Trematodes. Each is a deep, hemispherical, or subspherical cup, hollowed out in the side of the scolex, with circular (*Taenia*), oval, or even slit-like openings (*Moniezia*). No fusion of these suckers occurs, and it is quite exceptional that they are armed with hooklets (*Echinocotylidae*).

A new light has recently been shed upon the homologies of these organs by Pintner (34, *b*), who adduces evidence to show

that it is with the "accessory suckers," and not with the bothridia of the Tetraphyllidea, that they must be compared. They are, therefore, homologous with the "proboscides" of Tetrarhyncha. In a few cases, as *Anopl. perfoliata* (Fig. XXII. 6), vestiges of the phyllidia are believed to be represented by the ear-like flaps at the sides of the scolex, below the suckers.[1]

In the *Anoplocephalinae* the four suckers are at the apex of the scolex, the apertures being directed forwards, but more usually they are laterally placed, and a rostellum is present, which may be unarmed (as *T. saginata*) or armed, the armature consisting of from one to four circles of hooks, which are generally of two sizes,

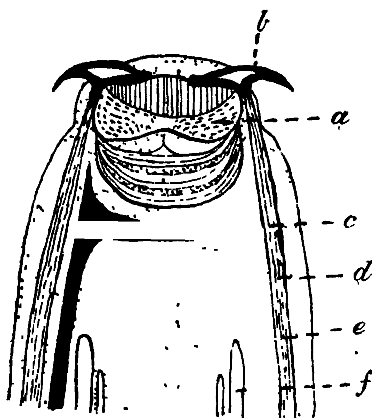


Fig XXIII

Longitudinal section of the rostellum of *T crassicollis* *a*, the muscular mass of the rostellum, below which are seen concentric coats of muscle, *b*, hooklet, *c*, ganglion and transverse commissure *d*, longitudinal (retractor) muscles of the hooklets, *e*, lateral nerve, *f*, excretory canal (After Leuckart)

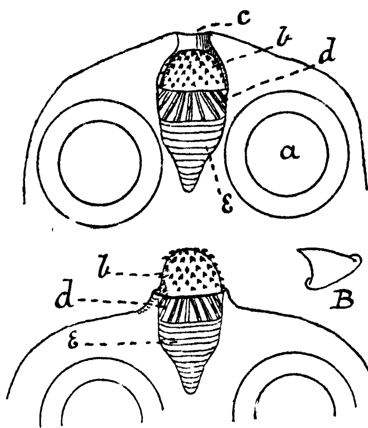


Fig XXIV.

The rostellum of *Dipylidium caninum*, L, out of the cat (orig), in the upper figure, retracted, in the lower, everted *a*, one of the suckers, *b*, the spiniferous region of the rostellum, *B*, one of the spines, *c*, the apical aperture on the scolex, through which the rostellum is everted, *d*, the region of longitudinal muscles, *e*, the region of circular muscles

arranged alternately (as in *T. solium*), the shape, size, and number of which afford valuable specific characters In its simple form it consists of a mass of muscles, acting on a cushion of connective tissue, bearing hooklets (Fig. XXIII.); this muscular mass becomes a hollow muscular sac, retractile into a pit (Fig. XXIV.). This armed rostellum reaches its highest development in those species of *Taenia* that inhabit birds, in which it consists of a muscular sac,

[1] The peculiar form *Polypocephalus*, Braun (?=*Parataenia*, Lint.), resembles the Tetracotylea in the arrangement of the acetabula; but is quite unique in possessing sixteen "tentacles," capable of being withdrawn into a sac in the centre of the scolex (Fig. XXII 5) They appear to represent a rostellum. The habitat, in *Trygon* and *Rhinobatus*, is exceptional for a Tetracotylean, and but little is known of the anatomy (Braun, 1878, and Linton (25), 1887).

bearing the hooklets at its apex; this rostellum is retractile into a second muscular sac, or "receptaculum rostelli." In other cases the rostellum carries a sucker. In any case the rostellum is retractile, and the arrangement of its musculature presents certain differences which appear to be characteristic of each sub-family (Lühe, 26).

In a few peculiar instances the scolex has been described as being absent, as in *T. malleus* and *Idiogenes otidis* (both rare forms), where the anterior proglottids become modified to form a "pseudo-scolex" (cf. *Thysanocephalum*). The size of the strobila, and the number of proglottids, exhibit that same range of variation referred to in the other groups; for instance, in *T. echinococcus* there are but

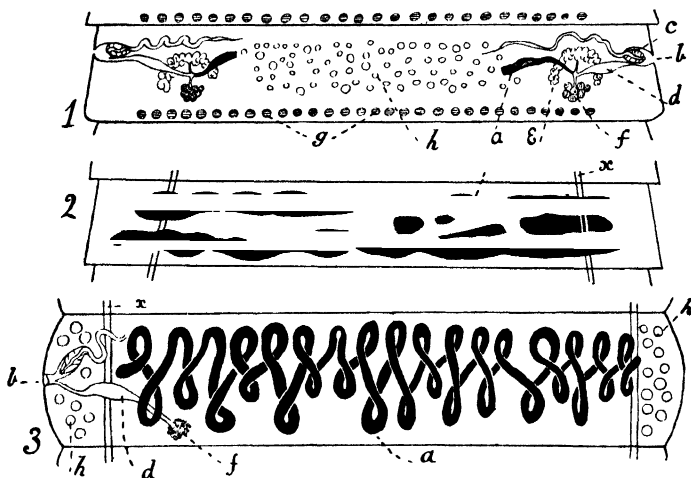


Fig XXV

1 A proglottid of *Moniezia expansa*, Rud (after Stiles and Hassall) 2 Mature proglottid of *Hymenolepis diminuta*, Rud (after Zschokke), out of the rat 3. Ditto of *Thysanosoma ovilla*, Riv, out of sheep *a*, uterus, *b*, genital pore, *c*, cirrus, *d*, vagina *e*, germarium, *f*, vitellarium, *h*, testis, *g*, proglottidean glands, *x*, excretory canal

four proglottids; in *T. saginata* 1200 or more The shape of the proglottids, both before and after separation, is also a valuable specific character, but here the development of the free proglottids, which, as a rule, drop off in groups,[1] is but slight, since the eggs in the uterus have already developed into hexacanth embryos before the separation. The shape too of the uterus, filled with ripe eggs, is employed as a specific character, while the egg coverings vary in each of the sub-families of *Taeniidae*.

The genital pore is marginal, but *Mesocestoides* forms an exception, the male and female pores being separate, and on the ventral surface. The genital pores, as in Tetraphyllidea, are either in the

[1] In *Anoplocephala* and *Drepanidotaenia* spp. no proglottids drop off. The strobila retains its entirety throughout life.

same margin throughout the strobila, when they are "unilateral" (on the left side in *Hymenolepis*), or in some proglottids they are on the right margin, in others on the left margin, when they are said to be "alternate"; but it is only rarely that there is any approach to a regular alternation. In opposition to what obtains in the Tetraphyllidea, the penis generally lies anteriorly to the vagina, except in *Ichthyotaenia* and *Mesocestoides.*

The female generative organs themselves present certain differences in structure and arrangement, as will be gathered from a comparison of the typical proglottids figured; but the most important difference is presented by the vitellarium, which, instead of being an extensive follicular organ, is—except in *Mesocestoides* and *Ichthyotaenia*, and some species of *Taenia*—a small acinous gland situated behind the germarium. The uterus, as in all the Tetrabothridiata, is a median sac, formed as an outgrowth of the germ duct; it is here more or less deeply notched, or even prolonged laterally into branching "egg sacs," the shape of the whole organ forming a specific character. In these forms, like *Moniezia*, with very short but wide proglottids, the uterus becomes transverse (Fig XXV.).

In some cases the wall of the uterus disappears as the eggs ripen, and these, either singly or in groups, come to lie freely in the parenchyma, the cells of which form capsules around each group (*T. dispar*, *Davainea*, etc.). In a few instances it is stated that the germarium actually becomes the uterus (*D. struthionis*).

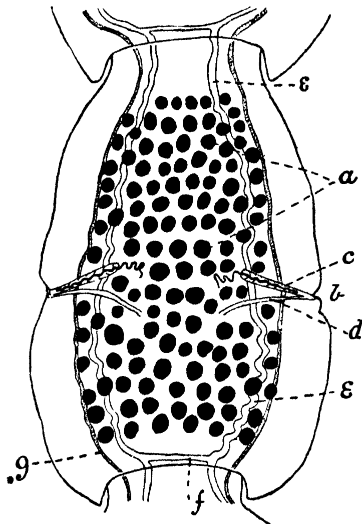


FIG XXVI.

A mature proglottid of *Dipylidium caninum*, L., out of the cat (Orig ×85) *a*, the uterus, here broken up on to a number of independent sacs; *b*, one of the pair of genital pores, *c*, the cirrus, *d*, vagina, *e*, the ventral excretory canal, *f*, the transverse canal, *g*, the lateral nerve

A very interesting phenomenon is the duplication of the genital organs (as in some species of *Bothriocephalus*), thus in *Moniezia* there are two complete sets of organs in each proglottid (Fig. XXV. 1), in *Dipylidium* the uterus is single, but the other organs are duplicated (Fig. XXVI.); whilst in *Amabilia* there is a single set of female organs, but two penes in each proglottid.

Life-history.—The segmentation of the egg and the development of the hexacanth embryo has been traced out by Leuckart, E. van Beneden, and Moniez,

but their interpretations of certain phenomena do not agree with one another, nor with those of Schauinsland for *Bothriocephalus.* The best general account is that of van Beneden for *T. serrata.* The egg, when it passes into the uterus, consists of the thin egg-shell, deposited in the ootype, surrounding a transparent non-cellular yolk, in which is embedded the egg-cell (Fig. XXVII.). The first segmentation gives rise to two blastomeres, one filled with refringent spherules (*b*), and the other faintly granular; the latter continues to segment, and ultimately three large cells (*c*) and numerous smaller ones are produced. The large cells increase in size and give rise to a "yolk envelope" enclosing the "granular cell" (*b*) and what remains of the original yolk (Fig XXVII. 2). The whole egg has greatly increased in size. The micromeres form a spherical

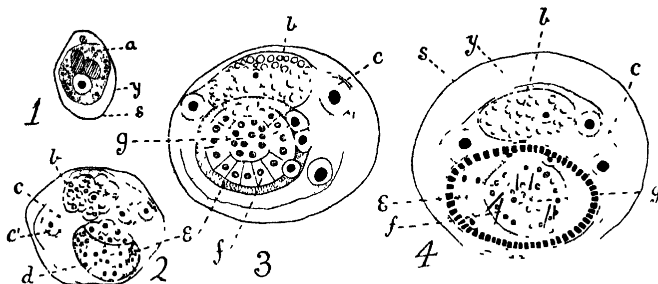


FIG XXVII —The early development of *T serrata* (after v. Beneden)

1 The unsegmented egg 2. Segmentation completed, the "chitinogenous layer" is growing over the embryo 3 The embryo exhibits an outer layer and central mass 4 The completed egg, with the six-hooked embryo within *a*, egg cell, at first containing yolk masses, *b*, one of the two first blastomeres, loaded with refringent spherules (which are not fat), *c*, the three macromeres, derived from the other blastomere, uniting to form the "albuminous coat" or yolk envelope, *c'*, their nuclei, *d*, embryonic mass, derived from the micromeres, *e*, chitinogenous layer, derived from some of these, which overgrow the embryo, giving rise to the striated coat in 4, *f*, outer layer (ectoderm) of the embryo, destined to give rise to the six hooks, *g*, the central (mesodermal) mass, *s*, shell, formed in the ootype, *y*, yolk, formed by vitellaria 1, 3, 4 are equally magnified 2 rather less

mass, and two cells at one end flatten out to form a cap; these cells divide further, and gradually enclose the remainder; the superficial layer of cells thus produced gives rise to a chitinoid coat; the central mass becomes the hexacanth embryo (Fig. XXVII. 4). This chitinoid coat, the homologue of the ciliated mantle of *Bothrioc. latus,* takes on a characteristic structure in each of the sub-families of the *Taeniidae* (Fig. XXVIII). In the *Taeniinae* it is striated; in the *Hymenolepinae* it is homogeneous and refringent (1, 2), while in the *Anoplocephalinae* it undergoes remarkable changes, becoming drawn out into two horns on one side, which may even cross, scissor-wise, forming the peculiar "pyriform apparatus" referred to above (Fig. XXVIII. 3, 4).

The development as far as this stage takes place in the uterus, while the proglottid still forms part of the strobila; and in the *Taeniidae,* and probably in all the Tetracotylea, the eggs of different

proglottids are in different stages of development, so that by examining the proglottids from behind forwards, earlier and earlier stages are met with independent of the time of the year, whereas in the Dibothridiata all the eggs in a strobila, at the same time of the year, are in the same stage of development. The general later history of the onchosphere, or proscolex, is as follows:—Ripe proglottids drop off from the strobila, and pass out of the host with its faeces; the proglottid either decays and sets free the eggs, which are then swallowed by browsing animals, or the proglottids themselves are devoured. But in order to attain maturity the egg of a given tapeworm must be devoured by a definite intermediate host (only in

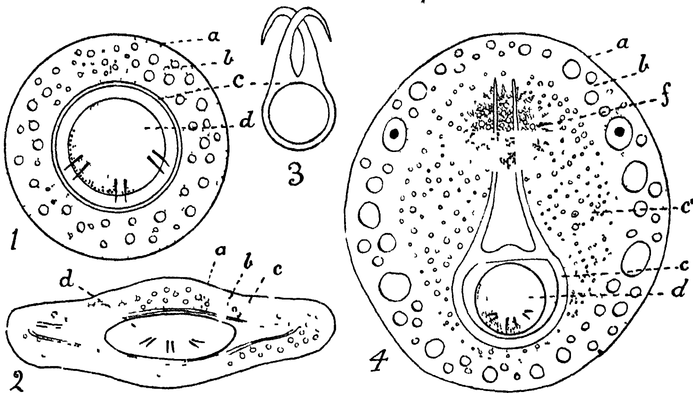


FIG XXVIII —Eggs of *Taeniidae* (modified from Moniez)

1 *Dipylidium caninum*, L 2 *Drepanidotaenia anatina*, Kr, from duck. 3. Pyriform apparatus of *Andrya wimerosa*, Moniez, out of rabbit 4 *Moniezia expansa*, Rud, out of ruminants *a*, egg shell (vitelline membrane of Moniez), *b*, albuminous coat, formed probably in all cases from some of the earliest formed blastomeres, two nuclei are represented in 4, the cells undergo histolysis, and become filled with refringent globules, *c*, internal shell, formed, according to Moniez, from modification of an outer layer of blastomeres, but possibly secreted by this layer (= striated coat of Fig XXVII), *c*, is the pyriform apparatus in 3, 4, *d*, the hexacanth embryo; *c'*, a "delaminated" layer of cells formed before the internal shell (*c*), according to Moniez, *f*, peculiar modification of this mass

a few cases do several different animals serve as hosts for one and the same worm) which is, as a rule, an herbivorous vertebrate, and in the majority a mammal, where the final host is a mammal; but in the case of bird and fish and amphibian tapeworms, the intermediate host may be some invertebrate.

Arrived in the intestine of the intermediate host, the egg-envelopes are softened and dissolved; the proscolex is thus set free, and by means of peristaltic movements, and by the movements of the six hooks it bores its way into the intestinal wall, and arrives in a blood-vessel (some constituent of the portal vein), in which it is carried along till it reaches a capillary of less diameter than itself. In this way it may be conveyed to the liver, peritoneum, mesentery,

or even the brain and eye; arrived here it may even burrow through the tissues on its own account. In any case it causes inflammation, and the tissues of the host give rise to a "cyst" around it. In this position it will undergo further development, resulting in a "metacestode" of one kind or another. This, when

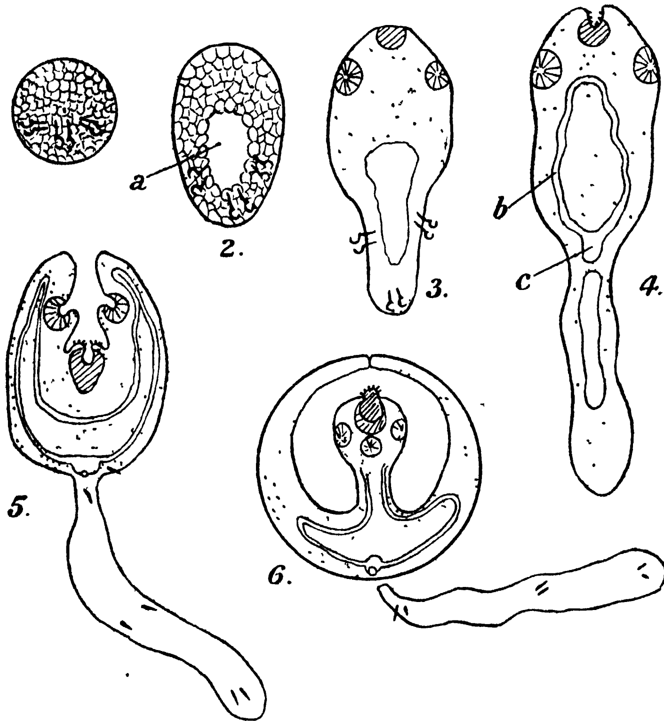


FIG XXIX —Development of *Dipylidium caninum* (altered from Grassi and Rovelli)

1 —Proscolex, onchosphere or six-hooked embryo, at present solid
2 —The embryo has elongated, and the "primitive lacuna" has arisen (*a*)
3 —The hinder part, bearing the hooks, narrows and elongates, so that a "head" and "tail" are distinguishable, at the anterior end the foundations of the four suckers and the rostellum are indicated—in reality at this stage they are mere solid heaps of cells
4 —The organism is longer, the body and tail are more distinct, the rostellum, now armed with spines, is cupped, as also are the suckers The excretory system is developed (*b*, *c*)
5 —The fore body is being invaginated into the hind body; the excretory bladder is provided with a pore at the base of the tail, the surface of which is shown with the scattered hooklets
6 —The tail has dropped off, a spherical "cysticercoid" remains, in which the "scolex" is commencing to grow upwards into the sac formed by the fore body, the outer wall consisting of the hind body.

swallowed by the final host, will develop into a tapeworm in the intestine of its new host.

One of the simplest metacestode conditions occurs in the case of *D. caninum* (*T. elliptica*), whose history has been worked out by Grassi and Rovelli (13). The eggs discharged with the faeces

become scattered amongst the hair of the dog, and are swallowed by its parasites, the flea (*Pulex serraticeps*) or the louse (*Trichodectes canis*), in the tissues of which the proscolex elongates; an excentric cavity ("primitive lacuna") arises by the liquefaction and degeneration of the internal cells, and the proscolex becomes pear-shaped, the hooks being at the narrow end (Fig. XXIX.). It is possible now to distinguish a "body" and "tail" (the "cystozooid" and "acanthozooid" of Villot). In the former a pair of excretory tubules make their appearance, which open by a median bladder and pore at the base of the tail. At the anterior end of the "body" the forecasts of the rostellum and the four suckers successively appear as cellular thickenings, followed by muscular differentiation, in the wall of the body; they mark out a "fore body" from a "hind body"; the tail, meanwhile, becomes constricted from the latter. The rostellum becomes pitted,[1] as also does each

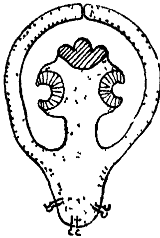


FIG. XXX.

The cysticercoid of *Hymenolepis murina* from the villi of the house's intestine (after Grassi and Rovelli) The tail is greatly reduced.

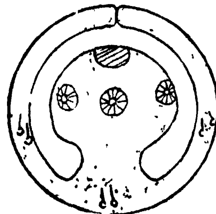


FIG XXXI.

Cysticercoid of *Dicranotaenia cuneata* which occurs in the earthworm *Allolobophora foetida* The tail and hind body have coalesced, the hooklets now appear on the wall of the small bladder.

sucker rudiment, and the whole fore body now becomes invaginated into the hind body. Meanwhile, the tail becomes larger and bladder-like, and in this way the hooks become separated, one pair remaining subterminal

The organism, before the invagination, resembles an immature *Caryophyllaeus*, or even a Trematode cercaria, in which as here the tail is a temporary larval organ.

The tail drops off when the intermediate host is swallowed by the dog; the "cystozooid," which is set free in the intestine of the latter, is a more or less spherical sac containing the invaginated head or "scolex," which nearly fills the cavity of the sac (Fig. XXIX. 6). Such a metacestode is known as a "cysticercoid" or parenchymatous bladder-worm. The head now evaginates, and its base commences to elongate and to become segmented to give rise to the strobila. The wall of the cysticercoid and of the following metacestodes is muscular, and contains lime cells and ramifications of the excretory

[1] Grassi homologises this pit with the buccal cavity and pharynx of Trematoda.

and nervous systems, which are absolutely continuous with the systems in the scolex. In this instance it is evident that there is a gradual metamorphosis of the proscolex into the scolex and neck of the strobila.

In *H. murina* the tail of the onchosphere is so reduced as to form part of the hind body, which envelopes the fore body or scolex, and the aperture by which the latter has been invaginated closes (Fig. XXX.).

A large number of other cases are known in which the invaginated scolex occupies almost the entire cavity (Fig. XXXI.). In some other tapeworms this cavity is larger, but filled with a loose tissue, as in the case of *Tetrarhynchus*, *Calliobothrium*, etc. But in the tapeworms of most mammals, e g. *T. solium*, this cavity becomes very much more extensive, since the six-hooked embryo

FIG. XXXII —The life-history of a *Cysticercus* (Bladder-worm, or hydatid) *a*, scolex, *b*, fore body, *c*, hind body+tail, caudal vesicle, or bladder.

1 —The solid proscolex.
2 —The primitive lacuna has formed as before, but the organism is greatly distended by the accumulation of fluid in this cavity The body and tail are no longer distinguished (cf Fig XXIX), and the hooklets have become cattered Excretory tubules have made their appearance in the wall of the "bladder"
3 —A further stage of this hydropic distention. An invagination of the wall of the bladder has arisen in the "fore body"
4 —The invagination proceeds, the suckers and rostellum arise by evaginations at the bottom of the tubular fore body, which hangs freely in the cavity of the cysticercus
5 —The scolex is commencing to evaginate, it rises up from the bottom of the "receptaculum scolecis" (or fore body), and at the same time the sides of the latter commence to evaginate.
6 —Eversion is complete—the sides of the fore body folded together, fuse to form the neck.
7 to 10 refer to *Taenia serrata* (after Leuckart)
7 —The entire bladder-worm, *Cysticercus pisiformis*, from the rabbit, with scolex everted, the excretory network in the wall of the bladder or caudal vesicle is shown
8 —The "bladder" (hind body+tail) has undergone digestion on reaching the stomach of the dog
9 —A further stage, in which the fore body is also destroyed, leaving only the "scolex."
10 – The scolex by elongation and "segmentation" of its neck has given rise to a young strobila

swells up by absorption of fluid [1] while encysted in the intermediate host (Fig. XXXII.) The hooks become scattered, and no "tail" is differentiated. Here, as in *H. murina*, the acanthozooid is not distinguishable from the cystozooid. Then there arises at one end a small tubular invagination (= the "fore body"), at the bottom of which the forecasts of the rostellum and suckers are formed. The "fore body" is here known as the "receptacle of the head," which in some cases, as *C. pisiformis*, may be very long. When this "bladder-worm" or cysticercus is swallowed by the final host the head (scolex) evaginates, and the original bladder (= "hind body + tail") which is now known as the "caudal vesicle," is digested, and the scolex gives rise to the strobila as before (Fig XXXII.).

This cysticercus leads on to another form of metacestode, with a still larger bladder, from the wall of which a great number of

[1] The fluid contained in a cysticercus is a weak saline solution containing ·2 to ·3 per cent of albuminoids, possibly nutritive.

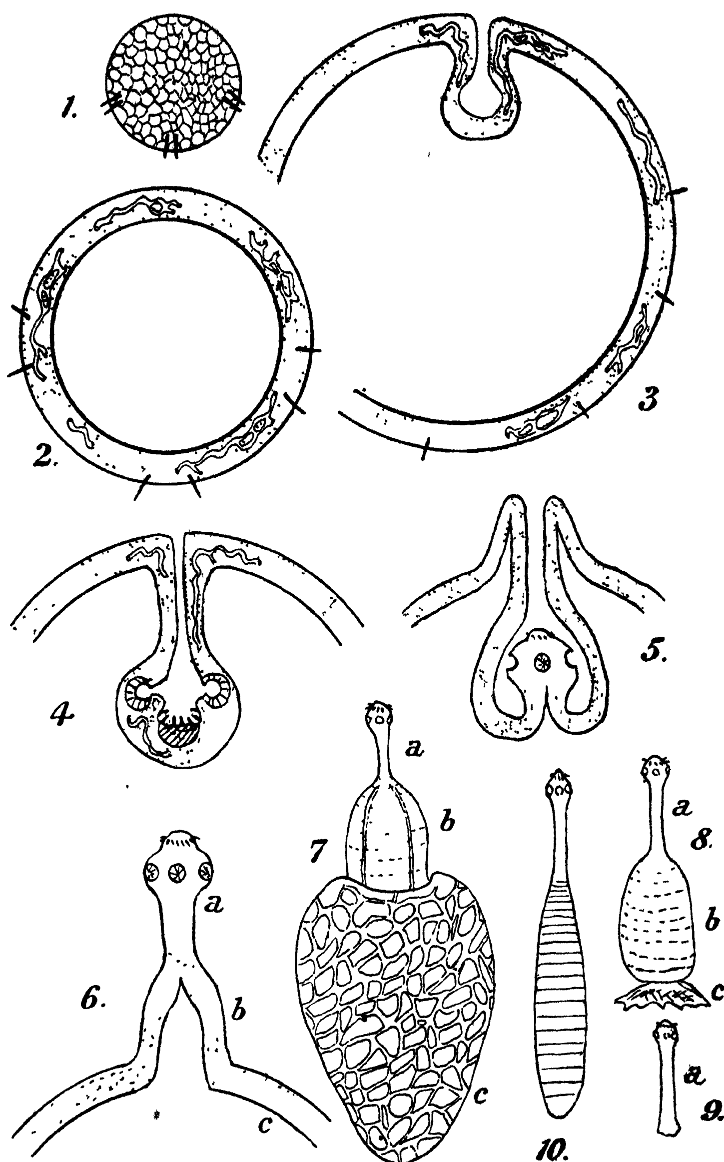


Fig XXXII.

heads are produced. This is the "coenurus" which occurs in the sheep's brain.

Just as the development of the head is delayed in these last forms, so apparently there is a delay in the differentiation of the fore body, for in *Monocercus* we have a bladder which "buds" off a secondary cyst within, from which the head is developed as before (Fig XXXIII. 1, 2, 3); while in *Polycercus*—occurring in Lumbricids, and which is the metacestode of *T. nilotica*, etc.—several such secondary cysts are formed, each with a head within it.

But this formation of secondary cysts reaches a maximum in "Echinococcus," where the primary bladder attains an enormous size, and from its walls numerous secondary bladders are formed, which drop off into the primary cavity (XXXIII. 5); from each of these secondary (and even tertiary) bladders a great number of heads are formed, each of which, when the bladders are swallowed, will develop into a strobila.

Fig XXXIII.—Asexual reproduction by the Bladder-worm.

1 to 3—*Polycercus*, from the coelom of an earthworm, it is the bladder stage of *Taenia nilotica*, out of *Cursorius europaeus* (Altered from Metschnikoff)

1—A cysticercus-like form, with five (or more) areas of proliferation on the wall of the bladder

2—Each of these becomes hollowed out to form a small sac, destined to drop into the central cavity Various stages of formation are shown (*a*, *b*, *c*)

3—After becoming free in the central cavity, each sac gives rise to head, and so becomes a cysticercoid as in previous cases

4—A *Coenurus*, from the brain of the sheep, the numerous scolices, of various ages, arise by invaginations of the wall of the bladder

5—*Echinococcus*, the secondary bladders arise at *a*, *b*, *c*, in the same way as the scolices in Fig 2 Each then develops numerous heads by eversion of the wall of the bladder, into which they may be secondarily withdrawn At *m* is shown the ideal mode of origin, so as to indicate the relation of head to daughter bladder, which is thus comparable to the "fore body" of cysticercus

6—A *Staphylocystis* (*S glomeridis*) as an example of external budding by a cysticercoid Each daughter cysticercoid develops a single scolex, the aperture of invagination of which is shown

In these latter cases—Coenurus, Polycercus, and Echinococcus—there is a process of gemmation, so that from each egg, not one only, but several tapeworms will arise. Another kind of asexual reproduction is met with in the case of a cysticercoid occurring in *Glomeris*, where by successive branching, and by the external gemmation of secondary cysticercoids, a complex organism, known as a "Staphylocystis," arises (comparable to the sporocyst of *D. macrostomum*), (Fig. XXXIII. 6).

In those metacestodes called "Urocystis," the tail of the original cystozooid drops off and becomes transformed into a second cystozooid, which proceeds to form a second scolex.

But even now that the life-cycle of these tapeworms is understood, and the relation of the "cystic" form, occurring in parenchymatous tissues, to the "segmented worm" living in the alimentary canal, is perfectly satisfactorily established, owing to the investigations of van Beneden, Kuchenmeister, Leuckart, and others, there still remains a matter which is even yet one of controversy, viz. to what degree does this history illustrate Steenstrup's *Theory of the Alternation of Generations.* Up till recent times the general opinion on the matter, founded as it was on an acquaintance

with the life-cycle of *T. solium* and similar forms, was that there are at least three different generations involved, viz. (1) the fertilised egg, which

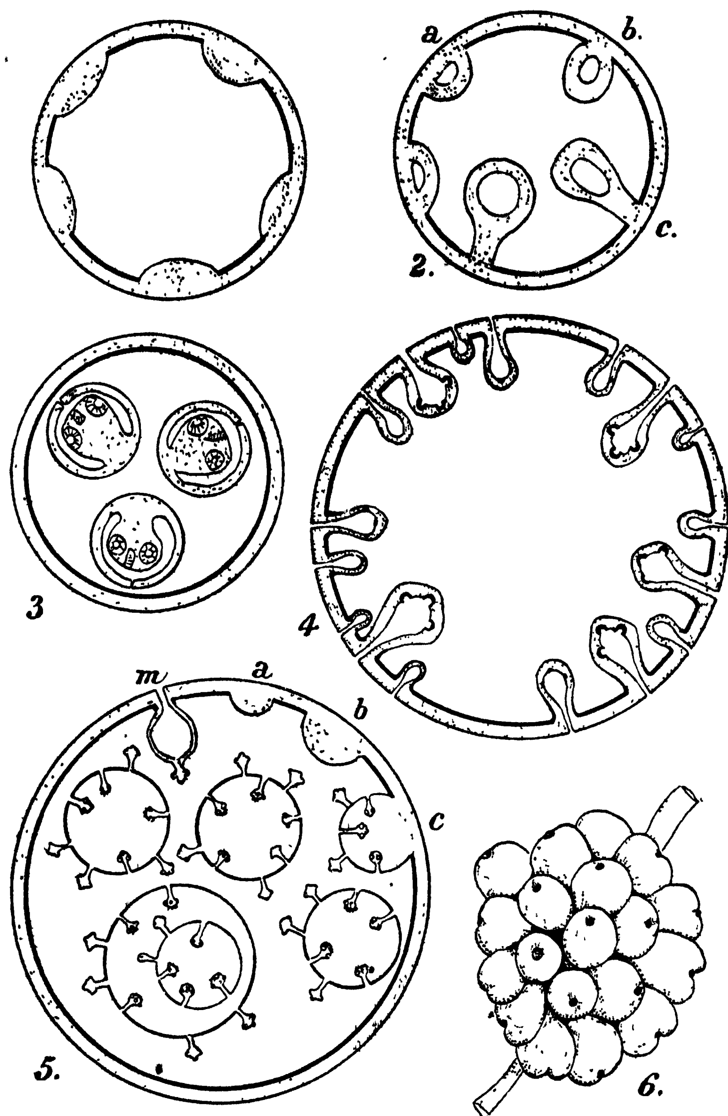


FIG XXXIII

gives rise by the ordinary process of development to a six-hooked embryo, or "proscolex," which becomes by modification the bladder-worm, *Cysti-*

cercus or "hydatid." (2) From the wall of this hydatid, or "nurse" (Steenstrup), the scolex is formed by internal gemmation. After being swallowed by the final host the bladder is destroyed, and (3) the scolex proceeds to produce by gemmation a series of sexual individuals—the proglottids—which produce eggs.

Recent investigations, both anatomical and embryological, however, tend to overthrow the view that the *hydatid* is a nurse, and that the scolex is produced from it by gemmation. Belief in this view was, to a great extent, fostered by the general custom of taking the life-history of *T solium* as typical, whereas there is little doubt but that the course of events exhibited by various cysticercoid forms is to be regarded as more archaic; where, that is, the scolex is merely a part of the proscolex, and becomes invaginated into the latter for the purpose of protection, in the same kind of way that the Amnion of the higher Vertebrates and of certain Arthropods has been brought about by the sinking of the embryo (Fig XXIX.); and possibly, lower than the cysticercoids, will be found some in which this invagination does not occur, as in *Caryophyllaeus*. It is, moreover, to be noted that the greatly developed "bladder" occurs in those tapeworms which inhabit the highest vertebrata, whereas in fish tapeworms the cysticercoid, under one form or another, occurs.

Granted that the scolex does not arise by any asexual mode of reproduction from the proscolex, it remains to be decided whether this asexual method can be allowed in the production of proglottids from the scolex—in other words, is the strobila to be regarded as a metamerically segmented *individual* comparable to an Annelid, or is it a linear *colony*, of which the *proglottids are the sexual individuals* produced by budding from an asexual scolex? The former view is held by Burmeister, Gotte, Claus, Perrier; the latter by von Siebold, van Beneden, Leuckart, and some of the older authors. Up till P J van Beneden's time the strobila was almost universally regarded as an individual, but his researches and his careful comparison of a proglottid with a Trematode, followed as it was by the observations of others, impressed naturalists with the idea that the strobila is a colony—a view which has been adopted generally up till about ten years ago, as it seemed to illustrate Steenstrup's theory so excellently. If we regard the tapeworm as a colony, it is comparable to the "strobila" of *Aurelia* and other Scyphomedusae, each ephyra, budded off from the original hydro-polyp or scyphistoma, being comparable to a proglottid, and the Scyphistoma itself, developed from the egg cell, being equivalent to the scolex If this be the case, the strobilation of Cestodes must be a secondarily acquired phase in their life-history, which must have been originally a metamorphosis, but owing to the individualisation of certain products of growth, it has given rise to alternation of generation (Claus, 6).

But many anatomical facts appear to be against the "colony" theory; the continuity of the muscular, nervous, and excretory system, not only throughout the entire adult worm and the scolex, but even in the cysticercoid phase, where they are absolutely continuous in the bladder and scolex. The excretory pore is at the posterior end of the proscolex, and in many adults it is at the posterior end of the chain throughout life, viz. in those forms which never drop proglottids, and though the development

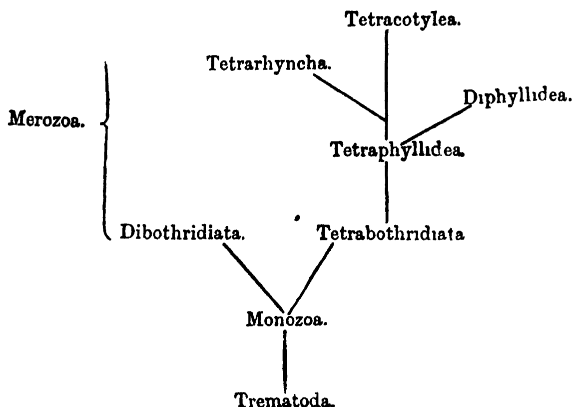
of these forms is not known in all its details, there can be no doubt but that the pore and contractile excretory bladder are identical at both stages of development. The permanency of the strobila in some worms, taken in connection with the absence of external segmentation in *Ligula* and *Triaenophorus*,[1] and the easy transition from the latter to the unsegmented Monozoa—these and sundry other facts seem to point most strongly to the individuality of the adult tapeworm.

It is not difficult to see the advantage to the species gained by this segmentation of the body as the genital organs ripen, for the continued peristalsis of the intestine, and the passage of food, must tend to rupture the attached worm. The scolex therefore regenerates this broken portion, as in various Chaetopods; and this power has been increased and perpetuated, so that the process of regeneration has become premature and resolved into one of "strobilation," or early production of segments, each of which ripens in turn and ultimately separates (Lang). This process is even more precocious in *Ligula*, where the repetition of the genital organs occurs in the intermediate host.

If the tapeworm be regarded as a metamerically segmented animal, the neck, as the point of formation of new segments, should be, in order to be comparable with the corresponding point in Annelids, posterior, *i.e.* antepenultimate, and the scolex or head must be the last segment or telson. This, indeed, is the view taken by Perrier and Moniez, who regard the "caudal vesicle" of *T. solium* and "tail" of *Caryophyllaeus* as the anterior end of the worm, though it is frequently assumed that the "tail" was originally an organ of locomotion, which function it has entirely lost, and has become in many cases part of the "bladder," and aids in protecting the enclosed scolex.

A curious theory was in early times held by several naturalists (Linnaeus, Dubois, Blumenbach) that the strobila is built up by the mutual attachment in series of numerous free-living proglottids, or *Vermes cucurbitini*.

The probable phylogeny of the class may be indicated by the following tree:—



[1] In the young *Triaenophorus* the proglottids are distinct; obliteration of them occurs as the worm matures.

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CHAPTER XX.

APPENDICES TO THE PLATYHELMIA.

APPENDIX I.

CLASS RHOMBOZOA, v. Ben.

THE forms included in this group are elongated, symmetrical organisms parasitic in the renal sacs of Cephalopoda. The body consists of a single layer of flat cells, which are usually ciliated, enclosing a central or "axial cell," within which the genital cells or "germs" are produced The ectoderm cells are specialised at one end, to form either a "polar cap" or terminal warts.

The individuals are of two kinds, producing different embryos—one, known as the "nematogen," produces "vermiform embryos"; the other, the "rhombogen," produces "infusoriform embryos."

The class Rhombozoa contains two orders

ORDER 1. **Dicyemida**, v Ben[1]

Adult forms worm-like and ciliated, with a polar cap formed of eight or of nine cells arranged in two circles

Dicyema, Koll., with eight polar cells, contains seven European species (Fig II.). *Dicyemennea*, Whitm.,[2] with nine polar cells; this genus includes three species.

ORDER 2. **Heterocyemida**, v Ben[3]

The ectoderm of the adult is not ciliated, there is no polar cap, but at the anterior end the ectoderm cells contain refringent bodies and may give rise to four large terminal wart-like papillae (Fig I).

Conocyema, v. Ben., in *Octopus vulgaris* *Microcyema*, v. Ben., without warts, in *Sepia officinalis*.

Remarks.—All the members of the Rhombozoa are parasitic in the renal organs of various species of Cephalopods; normally, the Dicyemids are attached, as was first observed by Wagener, by means of the polar cap to the renal cells which constitute the so-called "venous appendages."

[1] Ed. v. Beneden, *Bull. Acad. Roy Belge*, (2), xli. 1876, pp 85, 116, and xlii. p. 35; also in *Q J Mic Sci.* (N S), xvii 1877, p. 132.

[2] Whitman, *Mitth. Zool Sta. Neapel.* iv. 1883, p. 1

[3] E. v. Beneden, *Arch. Biol.* iii. 1882, p. 197.

They then have the appearance of small white threads; but on the death of the host the cells, with the parasite, drop off into the renal sac, where they are to be found swimming freely, but they never enter the various other cavities with which this renal sac communicates. The Heterocyemids do not appear to be thus fixed.

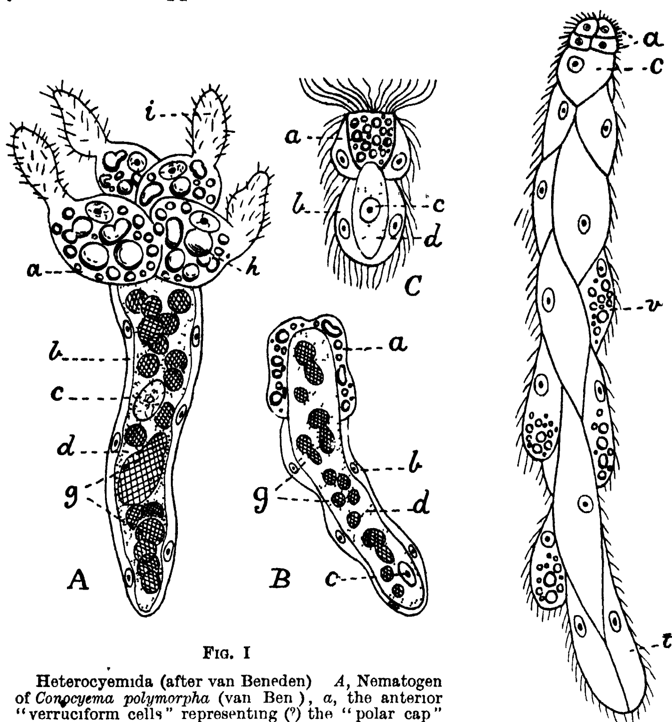


Fig. I

Heterocyemida (after van Beneden) *A*, Nematogen of *Conocyema polymorpha* (van Ben.), *a*, the anterior "verruciform cells" representing (?) the "polar cap" of Dicyemida; *h*, their refringent contents, *i*, "ciliated" processes (*N.B.*—The "cilia" are motionless and retractile), *b*, ectoderm cells of body, *c*, nucleus of axial cell, *d*, protoplasm of axial cell, *g*, germs, in outline, the largest being a fully formed vermiform embryo. *B*, Nematogen of *Microcyema vespa*, *a*, anterior cells with refringent contents, *b*, ectoderm of body, *d*, axial cell; *c*, its nucleus, *g*, germs. *C*, "Wagener's embryo" of *Microcyema*, *a*, cell (or cells) containing refringent bodies, *b* body ectoderm (of which there are only four cells in all), *c*, nucleus of axial cell (*d*) (The embryo of *Conocyema* resembles this in general structure, but is without refringent bodies, the cell (or cells) containing them being represented by four cells; there are also more ectoderm cells.)

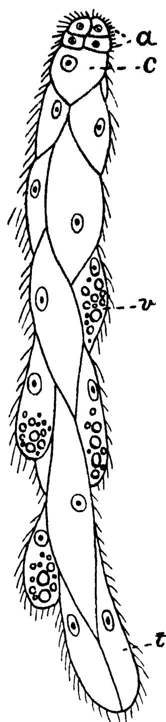


Fig. II

Dicyema typus, E. v. Ben. (after Whitman) Surface view of a young nematogen, from the left side, although cilia are indicated only round the edges, it is to be understood that the whole surface is ciliated. *a*, polar cells in two circlets of four, *c*, parapolar cells, followed by two dorsal and one ventral cell, *t*, terminal cells, which in some species may contain refringent bodies, which are here confined to the verruciform cells (*v*).

Leaving aside these aberrant and rare Heterocyemida, it is only necessary to describe the structure of the Dicyemida.

The elongated cylindrical body is pointed at one end, which is regarded as the posterior, while the anterior end is thicker, owing to the specialisation of certain of the ectoderm cells to form the "polar cap" ("calotte" of Whitman). The ectoderm is everywhere one cell thick, the

cells are flat, lozenge-shaped, or rhomboidal, and all carry cilia, which, on the "head," are shorter and denser than on the "trunk." The "polar cap" consists of two circlets of cells. The apical circlet always consists of four equal "propolar" cells (Whitman); the second circlet consists of either four "metapolar" cells (*Dicyema*), or of five cells (*Dicyemennea*).[1] The polar cells are symmetrically arranged in the young when the head is "orthotropous," but by the unequal growth of one, the dorsal, surface the polar cap becomes pushed forwards on this side, so as to lie more or less obliquely; it is then "plagiotropous" (Fig III). The polar cells, when eight, correspond in position, two of each circlet being dorsal and two ventral. In *Dicyemennea* the extra metapolar cell is dorsal (Fig. IV.). The whole organism recalls to some degree a Trematode "miracidium," and these cap cells remind one of similarly placed cells in such species as *Dist. tereticolle.*

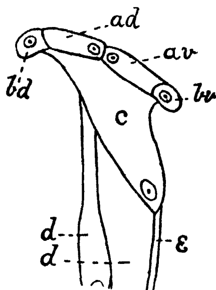


FIG. III.

Dicyema macrocephalum, E van Ben (altered from Whitman) A portion of a rhombogen seen from the right side; the plagiotropous cap is represented in optical section *ad*, *av*, dorsal and ventral propolar cells, *bd*, *bv*, dorsal and ventral metapolar cells, *c*, right parapolar cell; *dd*, the two dorsal, *e*, the ventral body cell

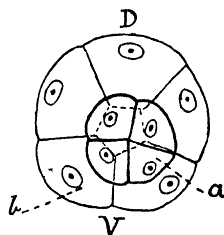


FIG IV.

Dicyemennea eledones, Wagen (after Whitman) The cap seen from in front, showing the five metapolars (*b*), of which three are dorsal and two ventral, *a*, propolar cell, *D*, dorsal, *V*, ventral surfaces

The first trunk cells lie one on each side, and as they differ somewhat from the rest, have been termed "parapolar" cells The next two are dorsal and ventral, the next couple are lateral, and so on throughout the body, though they are arranged somewhat spirally The two terminal cells differ slightly from the rest There are only some twelve to twenty trunk cells, exclusive of the parapolars

The contents of the cells, at first finely granular, soon exhibit in some cells coarser granules, and even crystalloid grains that may coalesce to form balls, which collect in these cells, and as they accumulate they form more or less pronounced swellings, or finally stalked sacs (Fig II. *v*); these "verruciform" cells never exceed six The nature of their contents is uncertain; they are neither fat nor lime, and do not take stains.

Within the ectoderm is a single "axial cell," from which, at an early stage in the life-history, germ cells are produced in such a way that they lie within the axial cell. The latter is derived from the larger of the first two blastomeres, but remains inactive till it has been sur-

[1] ἐννέα = nine.

rounded by the products of the micromeres (Fig. V.); then the macromere divides into two unequal cells; the larger again divides in the same way; so that the central mass at this stage consists of an axial cell with two small "primary germ cells," embedded in its cytoplasm one at each end. These primary germ cells are comparable to the "intermediate cells" of Orthonectida, but have a different fate. Here, in the Dicyemida, there is an early setting aside of cells for reproduction, just as there is in *Ascaris* and other higher forms. The axial cell remains apparently quiescent throughout life, but is possibly engaged in elaborating nutritious juices absorbed from the host by the ectoderm cells; it may be considered as an endoderm cell—the last representative of a degenerate enteron. But the primary germ cells soon divide, each into two, and then into four; so that there are eight germ cells lying within the axial cell.

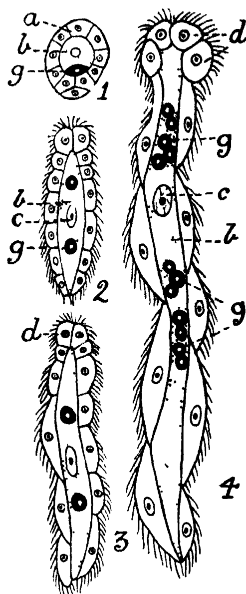


FIG. V.

Four stages in the development of a vermiform embryo of *Dicyema typus* (after E van Beneden) In 1 the result of segmentation is a solid blastosphere, consisting of a central macromere (*b*), and a peripheral layer of ectoderm cells (*a*), from the macromere a primary germ cell (*g*) has been given off In 2, 3, the embryo has elongated, the ectoderm is ciliated and already differentiated into cap cells (*d*) and body cells The germ cell has divided into two, and these have sunk into the substance of the axial cell In 4 the vermiform embryo has put on all the characteristics of a *Dicyema*, each of the two germ cells has already subdivided to form four, of which one above and two below are proceeding to develop into a second generation. *c*, nucleus of axial cell.

In some individuals (known as "nematogens") each germ cell proceeds to undergo segmentation, and develops into a "vermiform embryo" of a comparatively simple form—a miniature of the parent (Fig. V.). But in other individuals, known as "rhombogens"—differing, according to Whitman, in no definite way from the former—the germ cells pass through a very peculiar series of stages, and each produces a number of "infusoriform embryos" These two kinds of embryo were noted by Erdl, who regarded them as two different stages in the life-history. Kolliker was the first to recognise that they are dimorphic forms; while v. Beneden, and later, Whitman, more accurately traced out their development The vermiform embryos escape from the nematogen and swim about with their parents in the renal sac of the host, which they never leave; they are, indeed, killed by sea-water. They grow into nematogens, and repeat the history of their parent.

But the infusoriform embryo is a more complicated organism (Fig. VI.). It is nearly spherical, and built up of the following parts:—(1) Of an hemispherical cup of ten ciliated cells; (2) of two large cells containing refringent bodies, and occupying the "anterior" part of the surface of the

embryo; (3) of an "urn," which is partially enclosed in the preceding, but comes to the surface antero-ventrally. This urn, in its turn, is made up of (α) a "lid" or cover of four non-ciliated cells, which completes the outer wall of the embryo; (β) an "urn-wall" formed of two curved cells, laterally placed, underlying the ciliated cells; and of (γ) the "urn-contents"—namely, four granular cells, arranged crosswise; each has at first a single nucleus, but later many nuclei. According to van Beneden, these nuclei belong to minute cells provided with cilia, and he suggests that they are spermatozoa. This elaborate organism, or individual, arises in a very peculiar manner. Each germ cell divides, first of all, unequally, the smaller cell taking no further share in the process, but its nucleus enlarges, and lies freely in the axial cell; it is the "paranucleus" (Whitman), and is very suggestive of a polar body of metazoa in general The remaining cell proceeds to divide, very much as in the case of the vermiform embryo—one large cell becomes surrounded by a layer of smaller ones. This gastrula-like phase is termed an "infusorigen" by Whitman, and the central cell is the

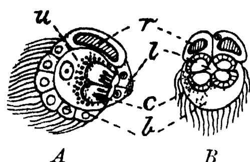


FIG VI.

Infusoriform embryo (or the male) of *Dicyema* (after van Beneden) *A*, from the right side, *B*, from the ventral surface, *r*, the refringent body, *u*, the capsule or wall of the urn, *c*, the contents of the urn (granular bodies), *l*, the lid, *b*, ciliated cells of the body wall (ectoderm)

"germogen." But this germogen proceeds to divide, endogenously, much as the axial cell of a vermiform embryo does, so that its nucleus becomes surrounded by a second generation of nuclei, each of which becomes invested by protoplasm to form a cell The "ectoderm" cells of the infusorigen separate, and each develops into an infusoriform embryo, which ultimately escapes from the rhombogen The remaining cells also separate, but develop into vermiform embryos, the central nucleus (germogen) remaining behind—free in the axial cell of the parent as a "residual nucleus" (Whitman)

The rhombogen, after the birth of the infusoriform embryos, becomes a "secondary nematogen," containing vermiform embryos. Thus there are monogenetic individuals (primary nematogens) and diphygenetic individuals which produce, firstly, infusoriform, and later, vermiform embryos The infusorigen is an embryo which gives origin to other embryos, much as has been shown to occur in *Gyrodactylus*. The infusoriform embryos escape from the parent, and, unlike the vermiform embryos, can live in sea-water (Erdl, van Beneden); but no changes of any kind have been observed in them, and their later fate is doubtful. But van Beneden, influenced by Metschnikoff's discovery of sexual dimorphism in the Orthonectida, and by Julin's observation of the two forms of females, suggested that the "infusoriform embryos" of Dicyemids are males.[1] Moreover, Whitman has occasionally observed in large specimens

[1] This appears to be confirmed by Wheeler (*Zool. Anzeig.* xxii. p. 169, 1899), who states that male dicyemids, *i.e.* infusoriform embryos are produced from

of *D. moschatum*, one or even two somewhat deformed infusoriform embryos, which he believes had penetrated into the nematogen. He is therefore inclined towards van Beneden's view. In that case, the nematogens will be females, and the germ cells true ova, which will be fertilised by the infusoriform embryos. It is, further, probably of some importance that in young Cephalopods nematogens predominate, while rhombogens are in excess in older hosts. But this is entirely conjectural. Nothing is accurately known about the fate of the infusoriform embryo, nor as to how new hosts become infected.

The view held by van Beneden that each species of Cephalopod has its own peculiar species of Dicyemid is not true. Whitman has noted both that two or more species of the parasite may occur in one Cephalopod, and that the same parasite may occur in different hosts; for example—

Dicyema typus, v. Ben. *D. schulzianum*, v Ben.	in *Octopus vulgaris*
D. moschatum, Whitm. *Dicyemennea eledones*, Wagen	in *Eledone moschata.*
D. truncatum, Whitm. *D. gracile*, Wagen.	in *Sepia officinalis*
D. truncatum, Whitm.	in *Rossia macrosoma*, *Sepia elegans*, *S. officinalis*

D. schulzianum, v. Ben., in *S. biserialis*, *Oct vulgaris.*

Class Orthonectida, Giard [1]

This group includes certain small ciliated organisms parasitic in some low invertebrates. These parasites are built up of an outer layer of flat ciliated cells, arranged in rings round the animal, and thus giving the appearance of segmentation, and of a central mass of polyhedral cells, which become ova or spermatozoa Between the ectoderm and the central mass are muscular fibrillae, having an obliquely longitudinal course The sexes are separate and dimorphic, the males being very much smaller than the females, from which they differ structurally. The females may themselves be dimorphic—one being cylindrical, the other flattened.

The group contains a single genus, *Rhopalura*, Giard, of which only three species are accurately known; *R. giardii*, Metschn. (= *R. ophiocomae*, Giard; + *Intoshia gigas*, Giard), occurs in the peritoneal cavity of *Amphiura squamata* *R intoshii*, Metschn (= *Intoshia linei*, Giard), in the body cavity of *Nemertes lacteus*. *R. pterocirri*, St J.,[2] occurs in the Polychaete, *Pterocirrus macroceros*. Further, a parasite was described by Keferstein in *Leptoplana tremellaris*, which no doubt belongs to the group.[3]

fertilised eggs; while females, *i e.* vermiform embryos arise parthenogenetically. Further, the same individual dicyemid may be at first a nematogen, and later a rhombogen.

[1] Giard, *Journ. anat. et physiol.* 1879, xv. p. 449; and *Q. J. Mic. Sci.* xx 1880, p. 225.

[2] St. Joseph, *Bull. Soc. Zool. France*, xxi. 1896, p. 58.

[3] Caullery and Mesnil have described a genus *Staechartrum*, from the Annelid *Scoloplos* (*C. R. Ac. Sc.* Paris, cxxviii. pp. 457 and 516, 1899).

R. giardii has been the subject of Julin's[1] researches, and is of more frequent occurrence than *R. intoshii.* The present account chiefly refers to the former species The male is minute and spindle-shaped (Fig. VII.). The ectodermal rings are six in number, including the anterior and posterior terminal cones. The whole body, with the exception of the second ring, is ciliated The cilia borne by the anterior cone are throughout the Orthonectida directed forwards, but elsewhere they point backwards. The third ring is larger than the others, but the second ring is noticeable for the refringent granular knobs borne by the cells. This ciliated ectoderm encloses the "testis," a mass of cells enveloped in a distinct membrane. In both sexes this central mass of cells, which give

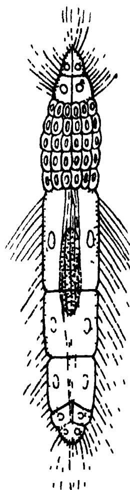


FIG. VII.
Rhopalura, male (after Julin).

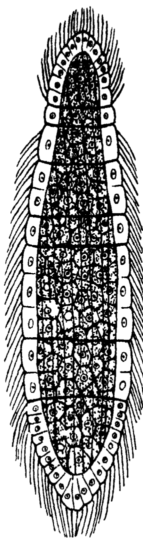


FIG VIII.
The cylindrical female of *Rhopalura* (after Julin)

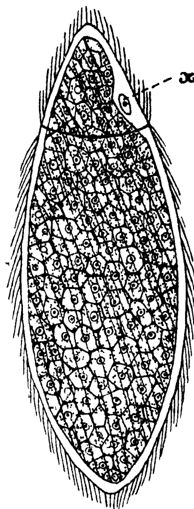


FIG IX
The flattened female of *Rhopalura* (after Julin) *x*, the peculiar subepidermic cell

rise either to spermatozoa or to ova, can be traced back, in the embryo, to a single axial cell, which, as in the Dicyemida, is the larger of the first two blastomeres into which the egg cell segments (Fig. X) But whereas in Dicyemida the genital cells are derived from a "primary germ cell" at each end of the axial cell, here the axial cell itself subdivides to produce germ cells, which represent, in all probability, mesoblast, whilst the last trace of "endoderm" has gone. Between the "testis" and the ectoderm a number of fine, obliquely directed streaks can be detected, forming a continuous sheath (Julin), or limited to four bundles (Metschnikoff). The ends of these fibrillae, which are regarded by Julin as muscular, appear to be continuous with ectoderm cells at each end of the body. Julin figures nuclei on them, superficial to the testis. Possibly they are

[1] Julin, *Arch. Biol.* iii. 1882, p. 1.

derived from the "intermediate cells," which have been sometimes noted in these positions. It has, however, been suggested that the "fibrillae" are merely the expressions of a folding of the testis-membrane.

The female is not only larger than the male, but differs so greatly from it that Giard referred it to a different genus, and described it under the name *Intoshia gigas.* Further, Julin discovered that there are two kinds of females—one flat, the other cylindrical. The cylindrical female presents eight rings (or, according to Metschnikoff, nine), (Fig. VIII.). Of these the second, as in the male, is not ciliated. The number of rows of cells differs in the various rings.

The flattened female (Fig. IX.) is broader than the cylindrical form, and presents no ectodermal rings. The ectoderm is formed of very flat cells, and is ciliated over its entire surface. There is at one point a sub-epidermal cell of considerable size, the meaning of which is obscure. It has been suggested that it represents a degenerated, obliterated enteron—in

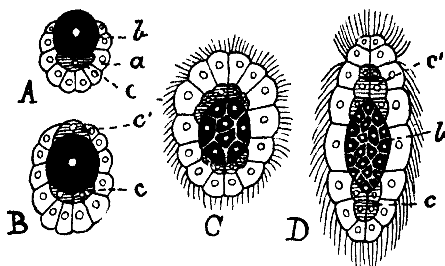


FIG X

Four stages in the development of the male of *Rhopalura* (after Julin) In *A* the macromere has become partially invested by the micromeres (*a*), and has already divided, giving rise to the primary germ cell (*b*), and to an intermediate cell (*c*) In *B* the macromere has again divided, giving off an anterior intermediate cell (*c'*) In *C* the central cells have become entirely surrounded by the ectoderm (*a*), which is ciliated The primary germ cell has subdivided and now constitutes the testis. In *D* the ectoderm cells have become differentiated, in that the cilia of the anterior cone are directed forwards, the rest backwards, the testis is assuming the condition of the adult, though the intermediate cells have not yet given rise to muscle fibres.

other words, it is hypoblast; but there appears to be no evidence in support of this view.

In both females the central mass consists of egg cells; these are free in the cylindrical form, and are discharged by dehiscence of the ectoderm at the level of the non-ciliated ring. They are fertilised by spermatozoa, and develop into males

The eggs of the flattened form are embedded in a granular mass, and develop parthenogenetically into females of either form

The females occur in a peculiar vacuolated mass of granular material in which no cellular structure is to be detected. This "plasmodial tube" (Metschnikoff, or "sporocyst" of Giard) fills up the body cavity of the host, but is enveloped in a nucleated layer, which appears to be part of the tissues of the host. Metschnikoff believed that both sexes passed their entire life in these "plasmodial tubes," but Julin has never detected males or embryos of males in them. These only occur free in the fluid of the body cavity.

These plasmodial tubes appear to be formed in this way:—The flattened females fragment; each piece, containing a number of eggs, rotates for a time in the cavity of the host, but later becomes attached to the wall of this cavity; the ectoderm cells now drop off, swell up, and undergo various changes resulting in the formation of the plasmodium. On the other hand, it is suggested by Max Braun that the latter arises by degeneration of the gonads of *Amphiura*, owing to the attacks of the parasite.

The development of the fertilised egg leads to a blastosphere consisting of a central macromere surrounded by ectoderm cells (Fig. X.); the former divides, twice, unequally producing a small cell at each end, whence the "intermediate cells" arise (cf. the primary germ cells of Dicyemida), the macromere now divides up into numerous germ cells. There thus appears to be no remains of an endoderm in this history; the macromere is mesoblastic, giving rise to muscular cells, and genital cells. In the history of the parthenogenetic eggs, the homologue of the terminal "intermediate cells" appears to be a continuous layer between the ectoderm and the axial cell, so that the two forms of females can be recognised at a very early stage.

[Caullery and Mesnil in the last three years (1898-1900) have described four new species of Orthonectids: (1) *Rhopalura metschnikovi*, parasitic both in a Chaetopod (*Spio martinensis*, Mes.), and a Nemertine (*Tetrastemma flavidum*). (2) *Rh julini*, parasitic in a Chaetopod (*Scotelepis fuliginosa*, Clpde). (3) *Rh. pelseneeri*, parasitic in *Tetrastemma flavidum*. (4) *Staecharthrum giardi*, parasitic in a Chaetopod (*Scotoplos muelleri*, Rathke) The two first-named species present distinct males and females as do the previously known species of *Rhopalura*. On the other hand, *Rh. pelseneeri* is hermaphrodite, as is also *Staecharthrum giardi*, which differs from all other Orthonectids by the great length of its filiform body. According to the observations of these authors (*Comptes rendus Acad. Sciences*, 20 février 1899, and later results privately communicated), which have extended to *Rh ophiocomae*, Giard, as well as the species above named, the plasmodium is a true protoplasmic nucleated structure, capable of amœboid movement. It is under this form that the Orthonectid makes its first appearance in the infected host. By segregation of certain of the nuclei and portions of surrounding protoplasm of the plasmodium, germ-cells are produced, and from these develop ciliated embryos which finally become adult males and females. The same plasmodium can give rise to both males and females. The sexual products of these ciliated offspring of the plasmodium are not discharged within the host, but only after the escape of the males and females into the sea-water. The sexually fertilised egg-cell and the resultant embryo are unknown, but it is this embryo which effects an entry into a new host and becomes a nucleated plasmodium which in turn again produces ciliated males and females. Thus there is an alternation of generations, sexual and asexual. The comparison of the plasmodium to the sporocysts of Malacotylous Trematoda by Giard appears to be justified, in so far that both are the first forms assumed by the sexually produced individual on entering upon parasitic life; and both give rise asexually

to numerous individuals which in some Malacotyla as in Orthonectida are destined to become sexually mature. Caullery and Mesnil consider that the plasmodium of the Orthonectida corresponds to the axial cell of the Dicyemida; the one as the other giving origin by endogenous germ-formation to sexual ciliated forms. According to Wheeler, the same axial cell of a Dicyemid produces successively females and males. There is therefore close agreement with the facts observed as to the "plasmodium" of the Orthonectida. Wheeler, however, suggests, but has not actually observed, that the males (so-called infusoriform embryos) of Dicyemids proceed from fertilised germ-cells only (see note, p. 152).—E. R. L.]

The Orthonectida and Dicyemida have been grouped together to form a grade Mesozoa by v. Beneden—a grade intermediate between the Protozoa and Metazoa, and characterised as containing multicellular organisms consisting of ectoderm and endoderm, the latter *not* being in the form of a layer surrounding an enteric cavity

But Giard, Whitman, and others have shown that the groups do not require the formation of this new grade to contain them; they are in reality Metazoa, for there can be no doubt but that the "intermediate cells" of Orthonectida and, at any rate, the "primary germ cells" of Dicyemida are mesodermic; possibly the axial cell of the latter represents an endoderm, reduced by parasitism to its last remnant—a single cell. In the Orthonectida, since the central cell of the embryo gives rise to genital cells, it may be regarded as mesoderm, so that in this group all trace of endoderm has disappeared Nor is this fact unique amongst parasites, for both in Cestoidea and in some Nematoidea the gut is entirely absent.

The simplicity of these organisms is not primitive, but secondary, they are degenerate Platyhelminths, but whether descended from Turbellaria or from Trematoda is uncertain; the resemblance to the ciliated embryos of the latter class is more apparent than real, for they are really much simpler than these.

Owing to the gap between these two groups and the rest of the Platyhelminths, Pagenstecher suggested the term "Mionelminthes" in place of "Mesozoa."[1]

APPENDIX II.

Trichoplax adhaerens, F. E Schulze,[2] occurs in the marine aquarium at Graz, and is known nowhere else. It is a small, circular disc, moving partly by means of cilia, partly by thrusting out simple pseudopodia-like processes. The organism consists of an outer layer of ciliated cells, but those on the lower surface, by which the animal creeps over the glass, etc., are columnar; those of the upper surface are flat The central mass of the body is composed of spindle-shaped and slightly branched cells, leaving spaces filled with fluid between them. Nothing is known of the process of reproduction beyond the fact that in autumn Schulze observed (1) that the individuals were drawn out into long threads, and

[1] Bronn's *Thierreichs, Wurmer.*

[2] *Zool. Anzeig.* vi. 1883, p. 92.

(2) there were numerous small circular discs in the water; he concludes that multiplication is effected by fission or fragmentation.

The homologies of the cell layers is uncertain; whereas some authors regard the columnar cells as endoderm, and look on the organism as a flattened-out gastrula, Butschli regards it as a "placula." There appears to be no reason to believe that the whole external layer is not ectoderm, but whether the internal tissue is mesoderm or endoderm, there is no evidence to show. Possibly *Trichoplax* is a degenerate, acoelous Turbellarian, deprived of rod cells.

Treptoplax, Korotneff, is somewhat similar, and has been seen in the Naples Aquarium.[1]

APPENDIX III

Pemmatodiscus socialis, Montic,[2] is essentially a gastrula, with ciliated ectoderm, containing rhabdites. One surface is flat, with a small central mouth leading into a distinct enteron. It occurs in cysts in the tissues of *Rhizostoma pulmo*, and appears to multiply by fission within the cyst; nothing is known of any "organs"

APPENDIX IV

What was termed *Salinella salve* by Frenzel, was stated by him to occur in a 2 per cent solution of salt at Cordova, in the Argentine. He describes it as an oval sac, with a wall formed of a single layer of cells, and containing a cavity communicating with the exterior at each end The "ventral" cells are ciliated, the dorsal are not ciliated but carry "setae," and all the cells are ciliated at their internal ends. Reproduction is said to take place by fission, and also by multiple fission after encystment and conjugation The "larvae" are declared to be unicellular likenesses of the "adult" and closely resemble hypotrichous ciliated Protozoa[3]

If *Salinella* has a real existence, it forms, as Apathy[4] has argued, an intermediate form between Protozoa and Metazoa, and the term Mesozoa has been resuscitated in this new sense. But there is not sufficient ground for accepting Frenzel's interpretation of his observations

So little is known about the anatomy or life-history of *Trichoplax*, *Pemmatodiscus*, and *Salinella* that it is impossible to make any definite statement as to their affinities Moreover, with the exception of *Pemmatodiscus*, they have only been met with in a "domesticated" condition in aquaria, and it has been suggested that they are in reality imperfectly developed animals—embryos which cannot attain full development owing to these conditions

[1] See Monticelli, *Mitth Zool Sta Neapel* xii. 1896, p 432

[2] Monticelli, *loc cit*

[3] *Arch. f. Naturges.* lviii. 1892, p. 71, and *Ann. Mag Nat. Hist.* (6), ix. 1892, p. 79.

[4] *Annals Mag. Nat. Hist.* (6), ix. 1892, p. 465.

CHAPTER XXI.

NEMERTINI.

PHYLUM RHYNCHOCOELA, MAX SCHULTZE

CLASS. NEMERTINI (von Siebold and Stannius).

BRANCH A. DIMYARIA.

Order 1. **Protonemertini**
Fam. 1. Carinellidae.
,, 2. Hubrechtiidae

Order 2. **Mesonemertini**
Fam. Cephalothricidae.

Order 3. **Metanemertini**
Fam. 1. Eunemertidae.
,, 2 Ototyphlonemertidae
,, 3. Prosorhocmidae.
,, 4. Amphiporidae.
,, 5. Tetrastemmatidae.
,, 6. Nectonemertidae.
,, 7. Pelagonemertidae.
,, 8. Malacobdellidae.

BRANCH B. TRIMYARIA.

Order 4 **Heteronemertini.**
Fam. 1. Eupoliidae.
,, 2. Lineidae

THE Nemertine worms constitute a compact group of animals distinguished alike from the lower Platyhelmia and from the more highly organised class of Chaetopoda by certain definite structural peculiarities.

Historical Survey.—The first account and figure of a Nemertine worm is given by Borlase in 1758. The early zoologists, such as O. F Muller, Johnston, Bosc, considered them as Turbellarians, and included them in

the genera *Planaria*, or *Fasciola*, or *Gordius*. And even when the anatomy of the group was better understood, they were retained as members of that class, though various positions were assigned to them within it. Thus, Ehrenberg placed them in his order Rhabdocoela; Quatrefages created an order Miocoela, which he placed side by side with the Rhabdocoela and Dendrocoela; Max Schultze divided the Turbellaria into (*a*) Proctucha, to include the Nemertines, which he termed Rhynchocoela; and (*b*) Aprocta, for the Turbellaria, s.s. And even in recent times this position has not been entirely given up, for Hatschek, in his Text-book, places the Nemertines in his group Autoscolecida, with the Platyhelmia, Rotifera, Nematoda, etc., all agreeing in the structure of the excretory organs.

On the other hand, some zoologists have exaggerated the resemblances to the Annelids which the Nemertines undoubtedly bear, and place them in this class (v. Siebold, Leuckart, M'Intosh). Lang includes them in his "Vermes," by which he understands the Annelids, Gephyrea, Polyzoa, Brachiopoda, Nematoda. The more recent authorities who have worked upon the group (Hubrecht, Burger) raise the Nemertines to an independent position between the Platyhelmia and the Annelida a view that was first taken by Cuvier, who formed the groups "Vers cavitaires" for the Nemertines, in opposition to the "Vers parenchymateux" (Platyhelmia), later, Blanchard invented the term Aplocoela, and Oersted followed in the same line. The interesting speculations of Hubrecht may here be referred to, viz. the suggestion that in the Nemertine various organs of the Chordata are represented, or are even anticipated in a humble fashion.

Amongst those who have added materially to our knowledge of genera and species reference may be made to the following —O. F. Muller, Oersted (34), Johnston, Keferstein (23), Stimpson, M'Intosh, Hubrecht, Joubin, and Burger; while Duplessis (13) and Guerne worked upon fluviatile species; Semper and Dendy (10) on terrestrial forms.

As contributors to our knowledge of the general anatomy of the class, the following deserve mention:—Quatrefages (36), Frey and Leuckart (14), Max Schultze (39), Keferstein. But all earlier writers are eclipsed by the brilliant monograph by M'Intosh (27), wherein he gives a critical account of all the earlier work on the subject Since that time Hubrecht and Burger have, by more modern methods of research, built up on this foundation a magnificent superstructure, culminating in the elaborate memoir by Burger, published in the series of monographs of the Fauna and Flora of the Bay of Naples

With regard to special points of anatomy, it is interesting to note that the eversibility of the proboscis was first noted by Davies (1815) on the addition of alcohol to water in which a Nemertine was living. Johnston was the first to recognise that in some Nemertines the proboscis is provided with a stylet, which is absent in others. But it was a long time before this proboscis and its sheath were properly understood; for by most of the earlier writers it was regarded as the intestine (Dugés, Ehrenberg, Quatrefages), while Oersted described it as a male copulatory

or excitant organ. Its true nature, and the fact that it is quite distinct from the gut, was first recognised by Frey and Leuckart in their account of *Lineus gesserensis* (1847), where, too, the real character of the mouth, hitherto regarded as the genital pore, was established.

The vascular system was recognised as a closed system of canals by Quatrefages (36); and our present knowledge of the comparative anatomy of the system is due to Oudemans (35), who in the same memoir gave an account of the excretory system in a variety of genera. This excretory system was originally described by Max Schultze in 1851 as a branched, ciliated canal; but it remained for Burger (7) to make the valuable discovery that these canals terminate blindly in a *multicellular* swelling, containing a flame, which had, however, already been seen by Silliman in 1885 in *Tetrastemma aquarum dulcium*, and was figured by Dendy in 1890 for *Geon. australiensis* (10).

The genital sacs were already known to Oersted, and the fact that the worms are dioecious was recognised by Quatrefages, and was a reason for separating the Nemertines from the Turbellaria. The nervous system was correctly described by Dugés (1828), who fell into the curious error of regarding the brain as a "heart," and the lateral nerves as "blood-vessels," owing to the fact that the system is tinged with red in the larger forms. Our present knowledge of this system is due to M'Intosh and to Hubrecht (17), while the finer histology of the system has been studied by Haller (16), and by Burger (6)

The cephalic fissures of the larger genera, such as *Lineus* and *Cerebratulus*, early attracted notice, but the function of the peculiar cerebral organs associated with them has been variously interpreted. Both Delle Chiaje and Hubrecht maintained that they were respiratory, while van Beneden took them to be excretory. The detailed account of these organs which we are now able to give rests upon the work of Dewoletzky (11) and of Burger (5).

But although the study of anatomy and histology has made much progress in these recent years, the embryology of the class still presents a wide field for future investigation. The Pilidium larva, originally described in 1847 by Joh. Muller (33), has been studied by several zoologists of note, especially by Metschnikoff (28), and by Butschli, and by Burger. The larva of Desor has been the subject of research by Barrois (1), and by Hubrecht (19), while the direct development of *Cephalothrix* has been studied by Dieck (12), and that of various other genera, quite recently, by Lebedinsky (26)

With regard to the taxonomy of the Nemertines, reference need only be made to three zoologists. Max Schultze (1853) divided them into two orders—the Anopla and Enopla This classification was generally adopted, till Hubrecht put forward his threefold division into Palaeonemertini, Schizonemertini, and Hoplonemertini, depending on the superficial position and diffuse condition of the nervous system in the first, on the cephalic slits in the second, and the armed proboscis in the third order. More recently Burger (8), laying stress on the relative depth of the nervous system, and on the structure of the body wall, proposed the four-fold division adopted in the present article.

The General Characters of the Nemertines.—These worms are, with a few exceptions, elongated, and subcylindrical in form, and marine in habitat. As in the Turbellaria, the epidermis is ciliated and the body is devoid of external segmentation. But unlike the Platyhelmia, the gut is provided with an anus, situated at the posterior end of the body (Figs. I., II., III.). The mouth, always anterior and subterminal, leads into a stomodaeum, which is, in the majority, a short, simple, cylindrical tube, leading to the enteron. The latter is a straight canal, usually provided with regularly arranged, paired, lateral diverticula. The most characteristic organ of the Phylum is the proboscis, which is a muscular pleurecbolic introvert, capable of eversion through an anterior terminal pore—the rhynchostome. This tubular proboscis is invested in an epithelium similar to the epidermis, containing rhabdites and nematocysts; and in one group calcareous stylets are carried on its wall in such a position that they lie at the apex when the proboscis is everted. In a state of introversion, the proboscis is contained in a closed tubular cavity, with a muscular wall—the rhynchocoel—lying above the enteron, extending for a vari-

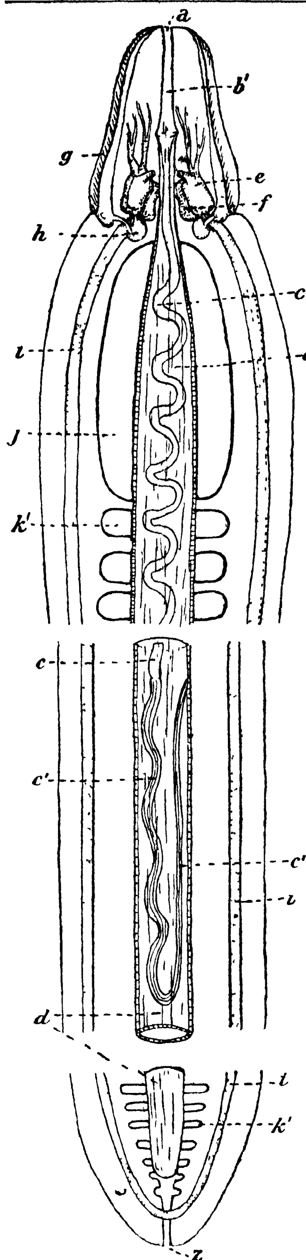


Fig. I.

Fig I

Diagrammatic view of *Cerebratulus*, as seen from above when the dorsal wall of the body has been removed, to show the proboscis and its sheath, the enteric and nervous systems, in the middle region the gut has been omitted *a*, rhynchostome, *b*, rhynchodaeum, *c*, proboscis, the tubular, eversible region, *c'*, the posterior, solid, non eversible region, which serves as the retractor muscle, *d*, rhynchocoel, *e*, dorsal ganglion, or lobe of the brain, the dorsal commissure has been removed, to show the continuity of proboscis and rhynchodaeum, *f*, ventral ganglion, or lobe of the brain, *g*, horizontal cephalic cleft, the depth of which is indicated, *h*, cerebral organ, the canal of which opens externally into the hinder end of *g*, *i*, lateral nerve trunk, *j*, stomodaeum, *k'*, intestinal caeca, *z*, anus

able distance along the body, and containing a corpusculated fluid.

The nervous system consists of a pair of lateral nerve cords running the entire length of the animal, and connected with one another at the hinder end, above the intestine (Fig. I.). At the anterior end each cord is enlarged to form a more or less complex cerebral ganglion, which is connected to its fellow by a dorsal and a ventral commissure embracing the proboscis. There is usually in addition a median dorsal nerve. The peripheral system is formed of a diffuse plexus, or of a more regular series of commissural nerves connecting the longitudinal nerves. On each side of the head there is, with few exceptions, a ciliated pit of simple or complex character—the cerebral organ—in close relation to the hinder part of the brain.

The excretory system (Fig. II.) consists of a longitudinal canal on each side of the stomodaeum, opening to the exterior by one or more short ducts, and at its inner end gives rise to a greater or less number of short, simple, or slightly branched tubules, each of which terminates in a multicellular swelling containing a bunch of cilia similar to the "flame" of the terminal cell of the Platyhelminth system (Fig. XXVIII).

There is in the Nemertines another system of tubes entirely shut off from every other cavity, and containing a corpusculated fluid, sometimes red in colour. This "vascular system" (Fig. III.) which is not present in the Platyhelmia, consists fundamentally of a pair of contractile lateral vessels extending the whole length of the animal, and connected with each other by a preoral and a supra-anal anastomosis. To this system there is usually added a median dorsal vessel, lying between the intestine and the wall of the rhynchocoel. In the majority of Nemertines these three longitudinal vessels are connected by transverse vessels more or less regularly arranged.

Between the muscular coat of the body wall and the wall of the gut is a loose connective tissue or "parenchyma," in which the excretory canals and the lateral blood-vessels are embedded. In it too the genital organs are developed. The sexes of the Nemertines are, as a rule, separate, and each genital organ is a simple sac, surrounded by a thin cellular membrane, which, at the breeding season, is prolonged outwards as a duct, to open externally above the lateral nerve. These genital sacs appear to be the only representatives of a coelom, and are repeated, more or less regularly, usually alternating with the intestinal pouches, throughout the body (Fig. II. *m*).

The development of the Nemertine is either direct or indirect; the larva is of a characteristic form, known as a Pilidium (or in a modified condition, as Desor's larva). In this larva

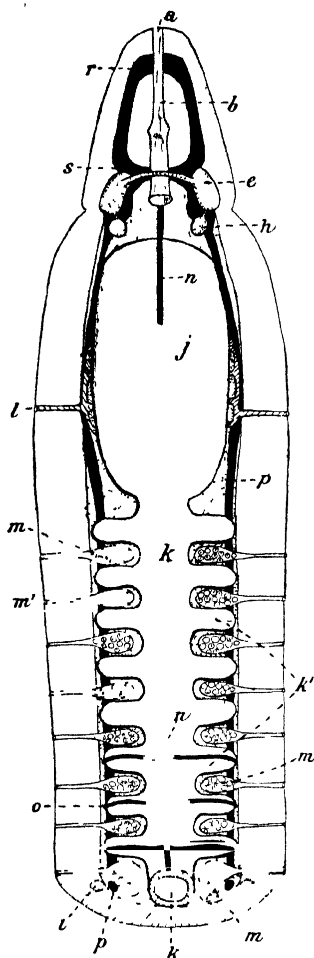


FIG II

Deeper dissection of the anterior end of *Cerebratulus*, after removal of the proboscis, and of the greater part of the dorsal blood-vessel. The lateral nerve trunks are omitted *a*, rhyncho-stome; *b*, rhynchodaeum, *e*, dorsal ganglion, or superior lobe of the brain, with dorsal commissure intact, *h*, cerebral organ, *j*, stomodaeum, *k*, intestine, *k'*, caeca, *l*, excretory pore, leading into the excretory duct, and thence to the branching canal, alongside the lateral blood-vessel, *m*, gonad (perigonadial coelom), *m'*, genital pore, *n*, dorsal blood-vessel, *o*, transverse vessel, *p*, lateral blood-vessel, *r*, *s*, anterior anastomoses

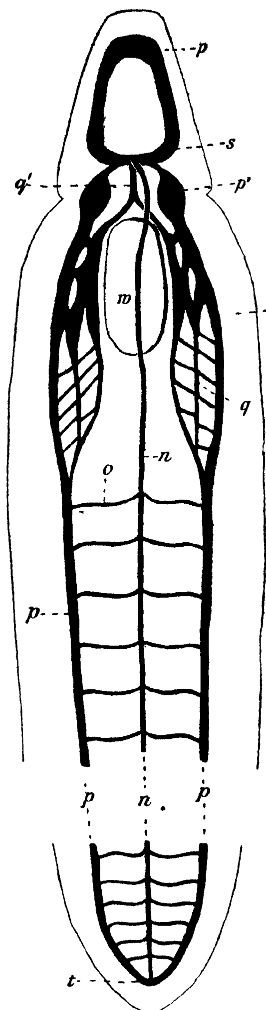


FIG III

Plan of the vascular system of *Cerebratulus*, from above *n*, dorsal blood-vessel, *o*, transverse vessels, *p*, lateral vessels, *p* (above), anterior, apical anastomosis, *q*, parastomodaeal sinus and network, *q'*, the median vessel giving origin to these, *s*, preoral anastomosis in region of brain; *t*, supra-anal anastomosis, *m*, mouth

the body of the Nemertine is formed, and the larval skin is cast off.

The result of the total and nearly equal segmentation of the egg is a blastula with a capacious blastocoel; the cells on one side are rather larger than the rest, and by their invagination the larva becomes a gastrula, which is at first uniformly ciliated.

A special tuft of long sensory hairs is developed in a pit at the aboral pole (Fig. IV.), and by the downgrowth of the sides of the body two or four great lappets are formed; the organism gradually becomes helmet-shaped (Fig. IV. *C*). The margins of these lappets

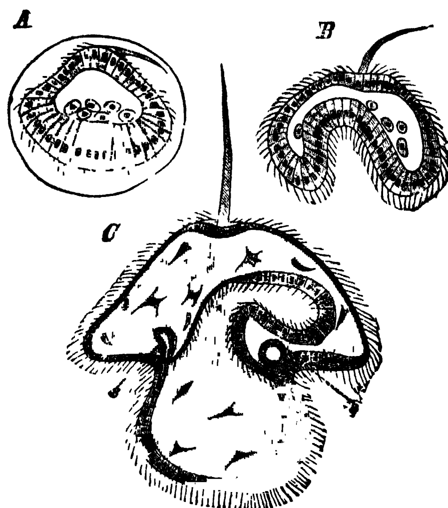


FIG IV

Development of the Pilidium larva (after Metschnikoff), from Joubin *A*, blastula, already ciliated and moving within the vitelline membrane, a few mesoblast cells have been given off by the blastoderm, *B*, the young gastrula, *C*, the larva The blastocoel is filled with jelly, in which mesoblast cells are embedded, the side walls have grown down into the right and left lappets, *s*, the anterior, *s'*, the posterior invaginations of the ventral surface which give rise to the "imaginal discs"

bear long cilia, which are continued round the whole of the ventral edge of the Pilidium, so as to form a circumoral band. Balfour has pointed out the phylogenetic significance of this larva, from which the Trochosphere of Annelids may have been derived. The Pilidium consists of epiblast, of hypoblast, and of mesoblast which gives rise to a jelly-like connective tissue between them. The greater part of the body wall of the future Nemertine is formed out of four invaginations of the ventral surface of the Pilidium —a pair of anterior or cephalic, and a pair of posterior or somatic pits (first recognised by Krohn and by Muller), (Fig. VI.). The wall of each pit soon becomes divisible into two regions—the

bottom is formed of columnar cells, and constitutes the "germ disc" or imaginal disc (cf. those of some insects). The outer walls consist of a flat epithelium. The aperture of invagination closes, and the pit becomes a sac, the thin wall of which is the "amnion" (cf. vertebrates and insects). These four flattened sacs sink inwards and extend laterally in all directions till they finally meet,

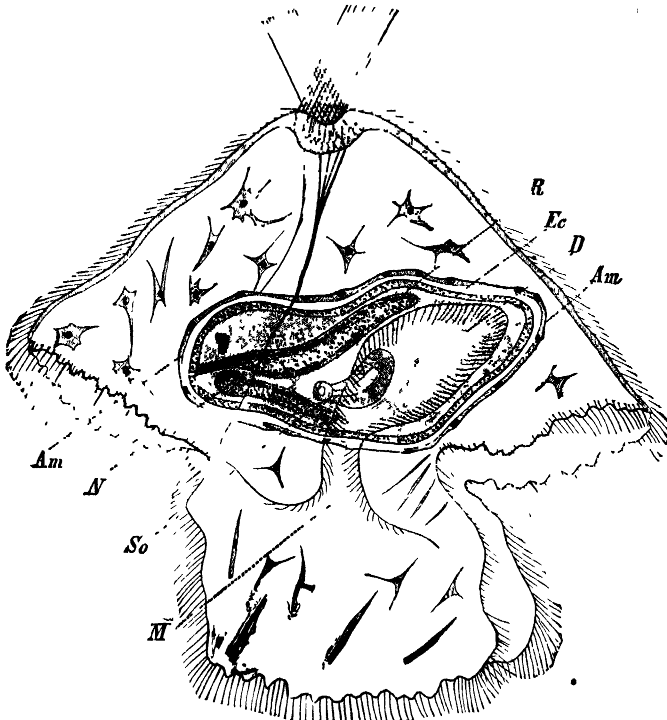


FIG V.

The fully developed Pilidium, bearing the young Nemertine within its amniotic sac (after Korschelt and Heider) *Am*, amnion, *D*, enteron of Pilidium and Nemertine, *Ec*, ectoderm of Nemertine, *M*, mouth of Pilidium, *N*, nervous system of Nemertine, *R*, proboscis, *So*, excretory organ

thus embracing the larval enteron and a certain amount of mesoblast, and giving rise to the body wall of the young Nemertine (Figs. V., VI.).

From the inner surface of the imaginal discs new mesoblast arises, thus a new body wall is formed within the larval skin. A fifth pit has meanwhile made its appearance at the anterior end of the larva, above the ciliated band; instead of flattening out as the others do, it elongates backwards to form a tube; it is the forecast of the proboscis (*Ra*). The

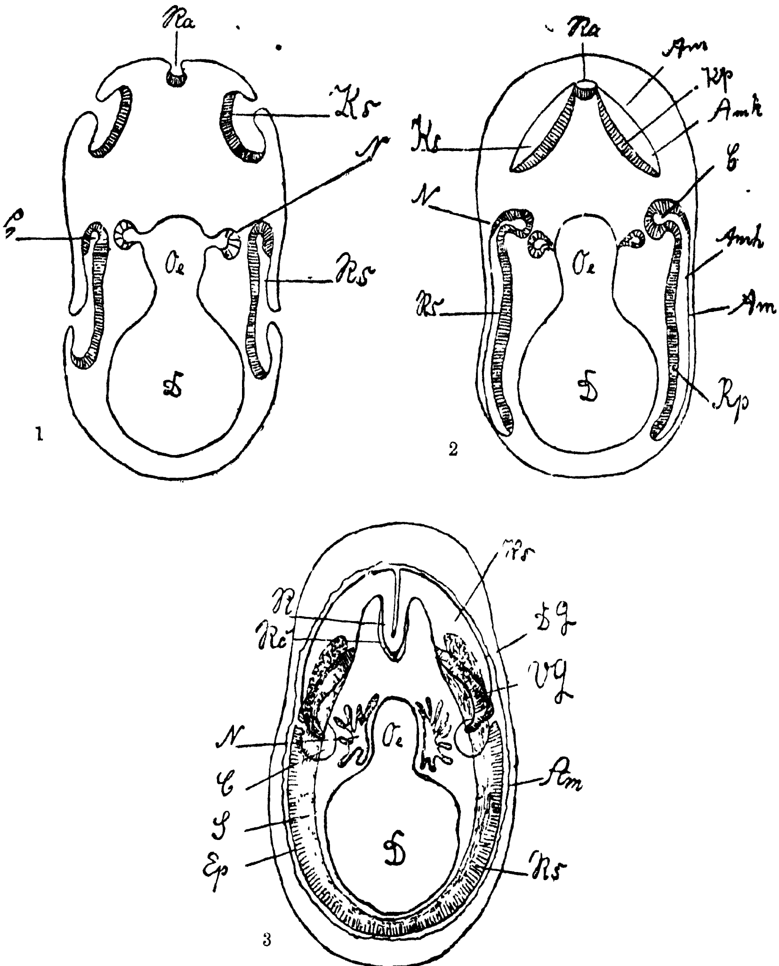


FIG VI

Three figures to illustrate the formation of the young Nemertine within the Pilidium (from Bürger) They are diagrammatic sections (or projections) across the larva, just above the origin of the lappets 1 shows the origin of the two pairs of imaginal discs, the pair of excretory pits (from the stomodaeum), and the median proboscis pit In each of the imaginal discs the bottom becomes thickened and the sides thin In 2 the imaginal discs are closed sacs (amniotic sacs), each is flattening and extending round the enteron of the larva, the cerebral organ is making its appearance 3, the imaginal discs have reached their fullest development, the new mesoblast has been given off, and the body wall of the Nemertine established The dorsal and ventral ganglia are defined (the cephalic "plates" are left unshaded to show these), and the excretory organ is branched *Am*, amnion, *Amh*, amniotic cavity, *C*, cerebral organ; *D*, enteron; *Dg*, dorsal ganglion; *Ep*, definitive epidermis of young Nemertine, *Kp*, cephalic plate, the thickened floor of the cephalic pit, *Ks*, cephalic pit, or imaginal disc, *N*, nephridium, or its foundation, *Oe*, larval stomodaeum; *R*, proboscis, *Ra*, invagination to form proboscis, *Rc*, the foundation of the rhynchocoel, its muscular wall, and the muscular coat of the proboscis; *Rp*, somatic plate, the thickened floor of the somatic pit, *Rs*, somatic pit or imaginal disc; *S*, lateral nerve stem of Nemertine; *Vg*, ventral ganglion.

mesoblast formed from its wall splits, giving rise to the rhynchocoel; the inner layer becoming the musculature of the proboscis; the outer layer the wall of the rhynchocoel or proboscis sheath.

The nervous system originates in two independent thickenings of the epiblast on each side; the dorsal lobe of the brain arises from the hinder part of the cephalic disc; the ventral lobe and the lateral nerve from the somatic disc. The cerebral organ arises as a secondary pitting at the anterior end of this latter disc (*C*).

The excretory system is epiblastic in origin, arising as a pit on the ventral surface of the larva, on either side of the stomodaeum (Figs. V., VI.). This undoubted epiblastic origin of the excretory system is of considerable general interest, since it confirms the view of Lang and others that the system in Platyhelmia is epiblastic, and provides some confirmation of Goodrich's distinction between a "nephridium" and a "coelomoduct." The blood-vessels arise as a liquefaction of the mesoblastic jelly

The Classification of the Nemertines.—Although the presence or absence of an armature on the proboscis is no longer regarded as of taxonomic value, yet the terms Anopla and Enopla may be used as descriptive, and contrasting epithets, in the same kind of way as "Invertebrata" and "Vertebrata," are used. Since Burger's classification is founded on the relation of the nervous system to certain tissues in the body wall, it is necessary to describe a transverse section of a Nemertine in this place, and *Carinella* is chosen as an example.

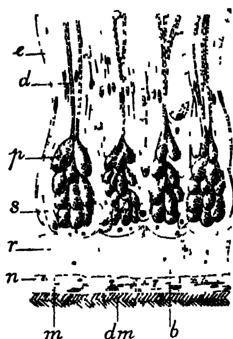


FIG VII

Epidermis of *Carinella polymorpha*, Ren (from Perrier, after Bürger) *b*, basement tissue, *d*, ducts of gland cells (*p*), *dm*, diagonal muscles (present only in large species), *e*, ciliated epidermal cells, produced internally into filaments, *m*, circular coat of muscles, *n*, nerve layer, *p*, grouped gland cells, *r*, radiating muscles in the basement tissue, *s*, club-shaped gland cells In the upper part, right side, is a "goblet cell," unlettered

The epidermis consists of a single layer of cells, of four kinds—ciliated cells, goblet cells, club-shaped gland cells, and grouped gland cells (Fig. VII.); below it is a basement tissue or cutis, then an outer layer of circularly disposed muscle fibres, followed by a deeper layer of longitudinal muscles (Fig VIII.). The parenchyma is thin in this genus, and below it is another layer of circular muscles (considered by Hubrecht as somatic, but by Burger as splanchnic), closely investing the enteron and the rhynchocoel. In the middle line, dorsally and ventrally, some muscle fibres pass from this layer to the cutis. The wall of the rhynchocoel consists of deeper circular muscles, to which longitudinal muscles are added.

In this transverse section the lateral and dorsal nerves (*e*, *j*) will be seen lying outside the circular somatic muscles, immediately

below the cutis. These nerves are connected by a nerve tunic, or plexus in this position, extending all round the animal. The brain likewise occupies the same relative position.

The characters upon which Burger chiefly founds his classification are (*a*) the somatic musculature, and (*b*) the relative position of the lateral cords. The dermal musculature consists either of two layers, as in *Carinella*, or of three layers, in which case a second coat of longitudinal muscles is developed in the cutis, external to the circular coat (Fig. X.). In these "trimyaric" Nemertines the lateral nerves lie between this secondary coat of longitudinal muscles and the circular muscles—that is, in the same

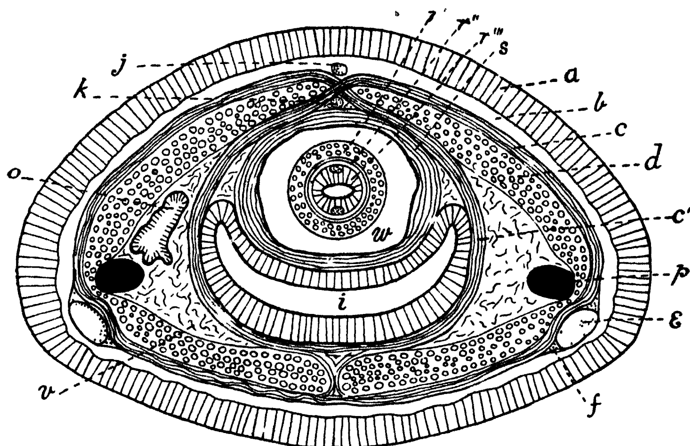


FIG VIII

Transverse section of *Carinella* (somewhat schematised, after Burger) *a*, epidermis; *b*, basement tissue (cutis), *c*, circular muscles, *c′*, inner (splanchnic) coat of circular muscles, *d*, longitudinal muscles, *e*, lateral nerve stem, *f*, portion of nerve network, *i*, enteron, *j* (superficial) dorsal nerve, *k*, proboscidial sheath nerve, *o*, portion of excretory canal, *p*, lateral blood-vessel, *r′*, longitudinal muscular coat of the proboscis, *r″*, circular coat, *r‴*, epithelium of proboscis, between these two last coats lies a nerve, above and below, *s*, the proboscis sheath, or muscular wall of the rhynchocoel (*w*), *v*, parenchyma

position, with regard to the latter, as in *Carinella*. But in the "dimyaric" forms the nervous system may either (*a*) lie outside the circular coat, or (*b*) in the substance of the somatic musculature, or (*c*) below it. in the parenchyma.

There can be no doubt but that the first of these three conditions is the most primitive, and the last the most recent; and the trimyaric arrangement has been derived from the dimyaric in another direction.

Using, then, the terms Anopla and Enopla as descriptive rather than as taxonomic terms, the Nemertines may be divided into two branches—the Dimyaria and the Trimyaria; and the former may be anoplous or enoplous, as follows:—

CLASS NEMERTINI, Siebold and Stannius, 1848

(= *Nemertina*, Ehrenb.; = *Nemertea*, Quatref.; = *Nemertinea*, Dies.; = *Aplocoela*, E. Blanchard; = *Rhynchocoela*, Max Schultze).

Branch A. Dimyaria. Nemertines in which the dermal musculature consists of an external coat of circular muscles and an internal coat of longitudinal muscles.

Section 1. Anopla, Max Schultze (= *Palaeonemertini* minus *Eupoliidae*, Hubr.). Dimyaric Nemertines in which the proboscis is not provided with a calcareous stylet; the mouth is behind the brain, and there is no anterior caecum to the intestine.

Order 1. **Protonemertini**, Burger.

Dimyaric anoplous Nemertines in which the brain and lateral nerve cords lie outside the musculature.

Family 1. Carinellidae, M'Intosh. The cerebral organ is in the form of a shallow vertical furrow, without any relation to the lateral blood-vessel; there is no dorsal blood-vessel The intestinal pouches are short and ill-defined. *Carinina*, Hubr.; *Carinella*, Johnst Family 2. Hubrechtiidae, Burg The cerebral organs are spherical and impinge upon the lateral blood-vessel A dorsal vessel is present; the intestinal pouches are deep. *Hubrechtia*, Burg.

Order 2. **Mesonemertini**, Burger.

Dimyaric anoplous Nemertines in which the lateral nerves have sunk into the somatic musculature.

Family—Cephalothricidae, M'Intosh. There is no cerebral organ nor cephalic furrow. *Carinoma*, Oudem.; *Cephalothrix*, Oersted.

Section 2. Enopla, Max Schultze. Dimyaric Nemertines in which the proboscis is armed with calcareous stylets, except in certain modified genera. The mouth is in front of the brain, and may be coincident with the rhynchostome The stomodaeum is complex, and there is usually an anterior, median, and ventral caecum to the midgut.

Order 3 **Metanemertini**, Burger (= *Hoplonemertini*, Hubr.)

The brain and lateral nerves have sunk through the somatic musculature and lie in the parenchyma. The mouth is in front of the brain.

Tribe A Prorynchocoela. Metanemertines with a long, thin body which can coil into a ball; they creep with eel-like undulations and never swim. The rhynchocoel never extends into the hinder half of the body, and the proboscis is much shorter than the worm.

Family 1. Eunemertidae, M'Intosh. Eyes present. *Eunemertes*, Vaill. (= *Nemertes*, M'Intosh *nec* Cuv.); *Nemertopsis*, Burger. Family 2. Ototyphlonemertidae, Burger. No eyes, a pair of otocysts. *Ototyphlonemertes*, Dies.

Tribe B. Holorhynchocoela. Metanemertines with usually a short body, which does not coil into a ball; they creep without undulations.

The proboscis is as long as the body. The rhynchocoel extending into the hinder third, and even to the end of the body.

FAMILY 3. PROSORHOCMIDAE, Burger. With four eyes, cerebral organs are rudimentary. Cephalic gland large. Mouth and rhynchocoel coincident. Usually hermaphrodite. *Prosorhocmus*, Keferst.; head notched anteriorly (Fig. IX.). *Prosadenoporus*, Burg.; *Geonemertes*, Semper, is terrestrial (10). FAMILY 4. AMPHIPORIDAE, M'Intosh. Eyes numerous. Cerebral organ large; the intestinal pouches are branched, and the gonads do not alternate regularly with them. The anterior caecum has long lateral diverticula. *Amphiporus*, Ehrenb; *Drepanophorus*, Hubr.; with unique armature to proboscis; the rhynchocoel is provided with metameric diverticula. *Zygonemertes*, Montg.; *Proneurotes*, Montg. FAMILY 5. TETRASTEMMATIDAE, Hubr. Small, flattish worms, with four eyes in a rectangle. *Tetrastemma*, Ehr; several fluviatile as well as marine species. *Stichostemma*, Montgomery; fresh water. *Oerstedia*, Quatref. FAMILY 6. NECTONEMERTIDAE, Verrill. Short, broad body, with "cirri"; tail with horizontal fin; apparently without stylets on the proboscis (see 41). *Nectonemertes*, Verr., 636 to 1735 fms. *Hyalonemertes*, Verr., 826 to 1641 fms. Atlantic. FAMILY 7. PELAGONEMERTIDAE, Moseley Pelagic, deep sea, transparent, leaf-like body, proboscis unarmed; no dorsal blood-vessel *Pelagonemertes*, Moseley; *P rollestoni*, M; South Sea, 1800 fms (Fig XI). *P. moseleyi*, Burg; S E. Japan, 755 fms *Pterosoma*, Lesson (see 20). FAMILY 8. MALACOBDELLIDAE, v. Kennel. Parasitic; short, compact body, with a posterior, ventral, glandular "sucker." The intestine is undulating without pouches or anterior caecum, the proboscis is unarmed. *Malacobdella*, Blv.; without eyes or cerebral organs. The proboscis opens into the foregut *M. grossa*, O. F. M. (Fig. XIII.); in the mantle chamber of various lamellibranch molluscs (see 24).

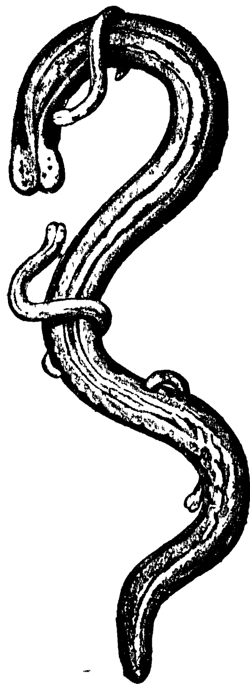


FIG IX

Prosorhocmus claparedii, Keferstein A viviparous Nemertine, with young (After M'Intosh, from Joubin)

BRANCH B. TRIMYARIA. Anoplous Nemertines in which a secondary coat of longitudinal muscles is developed outside the circular coat (Fig. X.).

ORDER 4. **Heteronemertini**, Burger (= *Schizonemertini*, Hubr. + *Eupoliidae*, Hubr.).

The lateral nerve stems lie between this secondary coat and the circular coat. The mouth is behind the brain; there is no anterior enteric caecum.

Family 1. Eupoliidae, Hubrecht. There are no lateral, horizontal, cephalic fissures. *Eupolia*, Hubr.; the head is sharply marked off from the trunk, into which it can be retracted. *Poliopsis*, Joubin; with a dorsal and a ventral median cephalic furrow, and a circular furrow between head and trunk. *Valencinia*, Quatref.; head awl-shaped; rhynchostome ventral. Family 2. Lineidae, M'Intosh. A deep, horizontal fissure on each side of the head, into the hinder end of which the cerebral organ opens. Group A. Amicrurae. Without a small, filamentous tail. *Lineus*, Sowerby; unusually long, thread-like body;

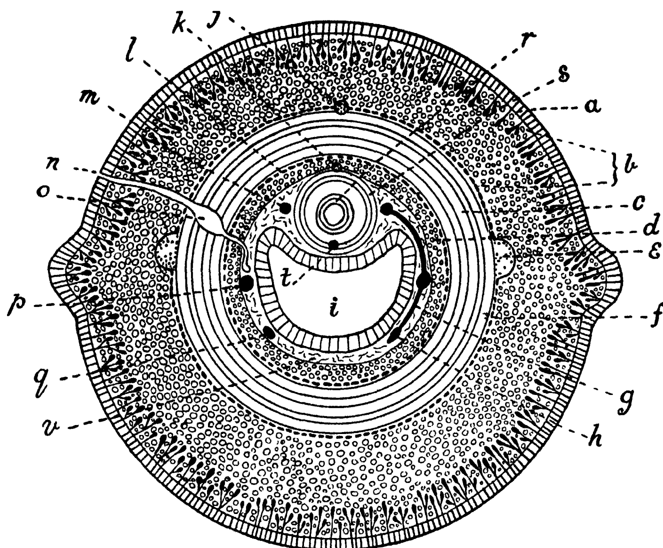


Fig. X

Transverse section of *Cerebratulus marginatus*, Renier (modified, after Bürger) *a*, epidermis; *b*, connective tissue or cutis, into which the epidermal glands dip, and which is occupied by the outer coat of longitudinal muscles, characteristic of the Heteronemertines, *c*, circular coat, *d*, longitudinal coat of muscle, *e*, lateral nerve stem, *f*, outer ring of nerve fibres; *g*, blood-vessel passing from lateral trunk to the parastomodaeal plexus (*h*), *i*, stomodaeum, *j*, dorsal nerve, *k*, proboscidial sheath nerve, *l*, deep nerve ring, *m*, vessel of proboscis sheath, *n*, aperture of excretory organ, *o*, excretory tube, receiving below one of the finer canals, *p*, lateral blood-vessel, *q*, parastomodaeal vessel, *r*, proboscis, *s*, proboscis sheath, the rhynchocoel is unlettered, *t*, dorsal blood-vessel, *v*, parenchyma.

head broad and spathulate. The animals cannot swim, but creep at the bottom or on the surface of the water, and can coil into clumps and balls. *Euborlasia*, Vaill.; body short, thick; contracts like a snail. Group B. Micrurae. With a small filamentous tail. *Micrura*, Ehrenb.; small, thin worms, unable to swim, but creep, coil into balls, and are contractile. Mouth small and circular. *Cerebratulus*, Renier; broad, strong worms, rolling up spirally and not coiling; they swim well, with eel-like undulations. The lateral margin of the body projects as a distinct ridge. Mouth long and slit-like. *Langia*, Hubr.; lateral margins curved upwards produce a deep dorsal groove; the margins are folded and lobed.

Remarks upon the Class.—The Nemertine worms usually live under stones, or amongst sea-weed, or in empty mollusc shells and similar places; some even burrow in the mud or sand, and a few secrete a tube of mucous material to which foreign substances adhere (e.g. *Carinella linearis, C. rubicunda, Valencinia longirostris*). The majority occur in shallow water, down to about 100 fathoms; only a few have been obtained from a greater depth, viz. *Pelagonemertes, Nectonemertes, Hyalonemertes,* and *Carinina grata,* at 1340 fathoms. These pelagic species, as well as *Cerebratulus,* spp., and *Drepanophorus,* are characteristically Arctic *Eupolia* is tropical. The non-marine forms are exclusively Metanemertines, some occur in fresh water, viz. *Tetrastemma,* sp. (13, 40), and *Stichostemma* (31), others live on land, viz. *Geonemertes,* of which five species have been described from various islands. A few live in association with other animals, and these again are Metanemertines, with the exception of *Cephalothrix galatheae,* which is endoparasitic in the ovaries of *Galathea strigosa* (12); others are ectoparasitic (3), or perhaps only commensals, viz. *Eunemertes carcinophila, Tetrastemma,* spp., on Ascidians; *Malacobdella,* in lamellibranchs (24) The Nemertines are generally cylindrical worms of considerable length, but of small diameter, exhibiting a great degree of contractibility; some indeed attain an enormous length, e.g *Lineus longissima* reaches a length of 8 or even 27 metres. On the other hand, a few species of *Tetrastemma, Oerstedia,* and *Ototyphlonemertes* are quite small. *Euborlasia* is an exception to the designation "long," as it is short and sausage-shape, like a Holothurian or Echiurid. *Drepanophorus* is relatively broad and flat as is *Malacobdella. Pelagonemertes* (Fig. XI.) is quite leaf-like (32). The colouring is often bright and of various tints; patterns are rare, either in the form of longitudinal stripes (*Micrura*), or combined with circular rings of lighter tone or different colour (*Carinella*). As a rule, the body presents no definite external regions, nor is it segmented; the hinder end is, however, generally narrower than the rest of the body, and more pointed than the anterior end which is truncated. In some of the Heteronemertines (*Cerebratulus, Micrura*) there is a distinct "tail," having the same structure as the body wall, but without gonads, and carrying the anus at its apex. Only in a few cases (*Carinella, Eupolia*) is the head definitely marked off from the trunk by a furrow (Fig. XXV.).

The mouth in the anoplous forms is some little distance from the anterior end of the body, and is situated behind the brain, but in the Metanemertines it shifts forwards so as to lie in front of this organ, and comes to lie close to the rhynchostome—in fact, in some species of *Amphiporus, Malacobdella,* and the Prosorhochmidae the two pores are coincident. The mouth leads into a "foregut" or stomodaeum, which in the Anopla is a tube of

relatively short extent; it has only a feebly developed muscular coat, and differs histologically from the enteron, which is directly continuous with it. In the Metanemertini, however, this foregut is much longer and divisible into the following regions:—(1) A narrow, buccal tube passing from the mouth as far as, or beyond the brain; (2) a dilated "stomach"; and (3) a narrow "pylorus

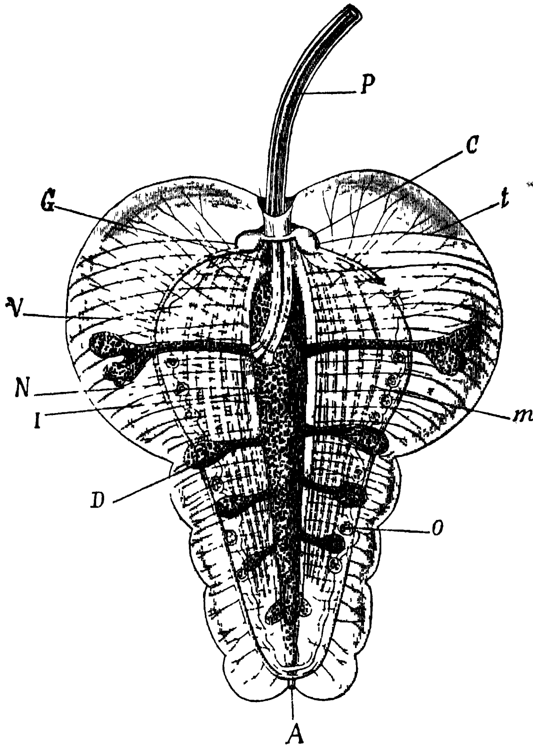


FIG XI

Pelagonemertes rollestoni, Moseley, dorsal view (from Perrier, after Moseley) *A*, anus, *C*, cerebral ganglion, *D*, intestinal caecum, *G*, rhynchocoel, *I*, intestine, *m*, longitudinal muscles; *N*, lateral nerve trunk, *O*, ovaries, *P*, proboscis, partially everted, *t*, circular muscles, *V*, lateral blood-vessel

tube"; both lined by gland cells (Fig. XII.). This last region opens into the enteron on its dorsal surface, so that there is a longer or shorter ventral "caecum" (*m*) differing in no way from the midgut itself. This caecum may, like the latter, be produced on each side into a series of diverticula. This caecum originally communicates with the exterior by means of the blastopore; when this closes, the stomodaeum, having arisen some little way in front of it (Lebedinsky), joins the enteron on its dorsal surface; whereas, in other

cases, the stomodaeum is formed in the blastoporal region. The enteron is in *Carinella* a simple cylindrical tube, which becomes slightly constricted, at intervals, by the developing gonads;

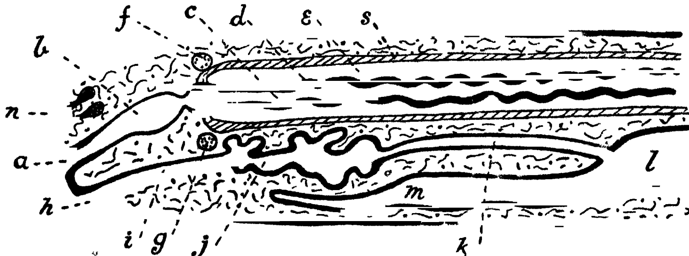


Fig XII

Diagrammatic sagittal section of *Amphiporus*, to show the median, anterior, intestinal diverticulum (*m*) of the Metanemertines *a*, rhynchostome, *b*, rhynchodaeum, *c*, cavity of the proboscis, *d*, muscular wall of proboscis, *e*, rhynchocoel, *f*, dorsal cerebral commissure, *g*, ventral cerebral commissure, *h*, mouth, *i*, buccal tube, *j*, "stomach"; *k*, pylorus tube, *l*, intestine, *m*, anterior caecum, *s*, muscular wall of rhynchocoel.

in *Carinina* and *Cephalothrix* these constrictions are more definite; while in the rest of the class longer or shorter pouches or diverticula are formed, which in some cases may even branch; they are separated from one another by dorso-ventral muscles forming more or less complete septa. There thus comes about a kind of metameric segmentation not only of the enteron itself but also of other organs, such as the gonads, which alternate with

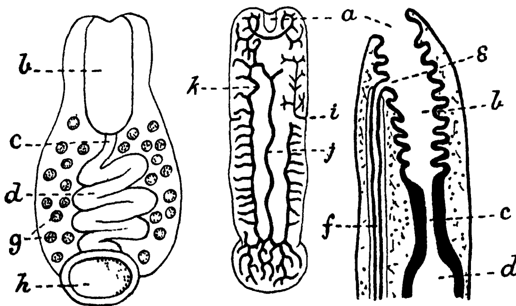


Fig XIII

Malacobdella grossa O F Muller (after von Kennel, Oudemans, and Burger) *a*, the mouth (dorsally situated), which is common also to the proboscis, *b*, the great "foregut" or "stomach", *c*, the pylorus tube, *d*, the intestine, *e*, rhynchostome, opening into the roof of the stomodaeum, *f*, proboscis, *g*, gonads, *h*, sucker, *i*, excretory pore, *j*, dorsal blood-vessel, *k*, lateral blood-vessel The figure on the left is seen from the ventral surface, the middle one from the dorsal, it illustrates the vascular and the excretory systems—the latter is indicated on the right side only,—and here a part of the lateral blood-vessel has been omitted, the left excretory duct and pore are shown

these pouches Only in *Malacobdella* is the intestine a simple tube, unconstricted by the gonads, and taking an undulating course from mouth to anus (Fig. XIII.). The anus is always small and terminal.

The integument of Nemertines consists of an epidermis resting upon a basement connective tissue, which is usually thin, but in Heteronemertini acquires a great thickness, and is then usually invaded by the outer longitudinal muscles. The epidermis consists of filamentous ciliated cells and gland cells of different kinds, of these the most peculiar are "grouped gland cells" (see Figs. VII. and XIV.), which are absent in Metanemertini.

That characteristic Nemertine organ, the proboscis, occurs in one of two conditions, as Johnston was the first to note; it may be unarmed, or it may be provided with calcareous stylets. In the anoplous forms (viz the Proto-, the Meso-, and Heteronemertini) it is a cylindrical, muscular tube, closed at its hinder

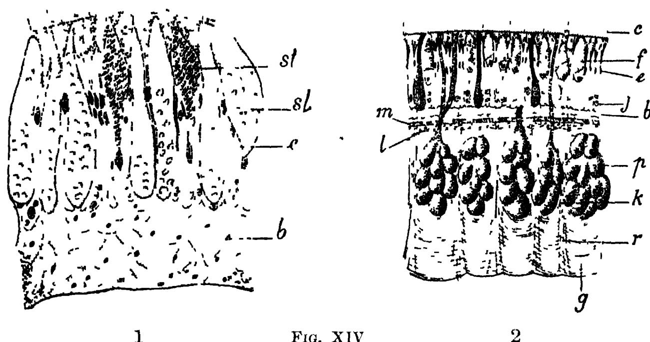


FIG. XIV

1, Epidermis of *Drepanophorus crassus* Quatrefages (from Perrier, after Burger) *b*, basement tissue, *e*, epidermal filament cells, *sl*, goblet cells with mucous contents, *st*, cells with refringent, rod-like contents 2, the integument of *Eupolia delineata*, D Ch (from Perrier, after Burger) *b*, basement membrane, *c*, cilia, *e*, epidermal (filamentous) cells, *f*, goblet cell; *g*, connective tissue forming the cutis (in most Heteronemertines this cutis is invaded by the outer longitudinal muscles), *j*, interstitial nuclei, *k*, partitions between the groups of gland cells, *l*, subepidermal layer of longitudinal muscles, *m*, subepidermal layer of circular muscles, *p*, packets of gland cells, sunk in the cutis, *r*, radial muscle fibrils.

end but open anteriorly, its wall becomes continuous with the body wall at about the level of the brain. This precerebral region is termed the "rhynchodaeum," and opens at the apex of the head by a small round pore, the "rhynchostome." Behind the brain the invaginated proboscis lies in a closed tubular cavity, the "rhynchocoel," with muscular walls, to which it is attached, somewhere near the hinder end, by the retractor muscle (Fig. I. *c*, *c'*). A transverse section of the proboscis shows the following layers of tissue:—internally (at rest) it is lined by tall columnar and glandular cells, similar to those of the epidermis, from which, indeed, this epithelium is derived during embryogeny; these columnar cells are arranged in groups and clusters, forming wart-like papillae of various shapes and character, diagnostic of species. In most genera these cells contain "rods" similar to the "rhabdites" of

Turbellaria; to these are added, in *Cerebr. urticans*, nematocysts like those of Coelenterates, except that several are contained in each cell. Below this is a basement membrane, then follows the musculature, which in general repeats that of the body wall, only reversed, being "dimyaric" in the Proto- and Meso-nemertini, and "trimyaric" in the Heteronemertini. Outside, again, comes the flat rhynchocoel epithelium. Behind this tubular, eversible region the circular muscles cease; but the longitudinal muscles are continued backwards to form a "retractor muscle" In *Eupolia* this

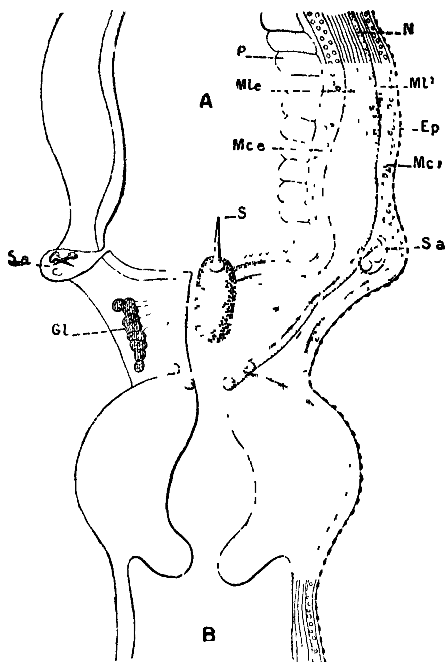


FIG XV

Proboscis of Metanemertine Longitudinal section in the "middle" region in a state of retraction (from Joubin) *A*, the cavity of the anterior region, capable of eversion; *B*, cavity of posterior, retractor region The cavity of the middle region is unlettered, it consists of a dilated "reservoir" communicating by a "duct" with the anterior region The plane in which the nerve rings lie is the "diaphragm" *Ep*, epithelium of rhynchocoel, *gl*, gland cells, whose ducts pass to the "acanthophore," which they probably secrete, *Mce*, layer of circular muscles, which are external on evagination, *Mci*, layer of internal circular muscles, *Mle*, layer of longitudinal muscles, external on evagination, *Mli*, internal longitudinal muscles, *N*, nerve layer in proboscis, it is continued down to the diaphragm, when it forms two rings round the "duct" *P*, the epidermal papillae, *S*, the median (functional, or chief) stylet, supported on its acanthophore, which is unlettered, *Sa*, right and left "acanthocysts" containing lateral, reserve or accessory stylets.

retractor muscle is hollow, the narrow tubular cavity being continuous with the wider cavity of the proboscis proper; there are thus in this genus two tubular regions to be distinguished in the proboscis—an anterior eversible region, and a posterior non-eversible region. This leads on to the more complicated apparatus of the Metanemertines (Fig. XV.). Here the two regions are quite definite, and are separated by a third, middle region in which the calcareous stylets are developed. The wall of this middle region is much thickened, owing to the development of special muscles and of gland cells; the canal which puts the anterior and posterior cavities into communication is differentiated into three parts: (1)

the posterior part is termed the "canal"; this dilates to form (2) a "reservoir" or bladder, which communicates with the anterior chamber by means of (3) the "ductus ejaculatorius," which traverses the "diaphragm" or anterior part of the middle region. On the anterior face of this diaphragm are set the "stylets"; these are solid, calcareous spines (containing organic matter), generally shaped like a tin-tack; of these, one is median and fixed at the bottom of a funnel-shaped depression, by a somewhat conical, granular mass, formed by the secretion of gland cells in the diaphragm; this is the "basis" or "acanthophore." On each side of this median stylet (*Begriffstilet*, of Burger) is a small sac containing two or more lateral stylets, differing from the median one in the absence of the acanthophore, and somewhat also in size (Fig XVI.).

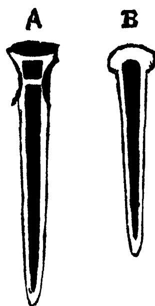


Fig. XVI
Stylets of *Amphiporus* (from Joubin, after Montgomery) *A*, a lateral stylet, *B*, a median stylet

In *Amphiporus*, alone, are there more than two sacs of lateral or accessory stylets; in this genus five, or seven, or even twenty-two sacs may be present. Each sac of lateral stylets opens into the anterior proboscis cavity by a short duct. According to Burger, each of these sacs is an enormous cell, in which one or more calcareous stylets arise in vacuoles—each commencing as a small spicule and soon attaining its full size. These cells (or sacs) may be termed "acanthocysts," and each is comparable to a "rhabdite cell" or "sagittocyst," from which they may possibly be descended. It is supposed that these lateral or reserve stylets are destined to take the place of the median one when (and if) this be lost.[1]

This arrangement of stylets obtains in all the armed Metanemertines with the solitary exception of *Drepanophorus* (Fig. XVII). Here the "acanthophore" is a long, narrow, curved plate bearing as many as twenty short, conical stylets arranged in a row, so that the apparatus appears to be used rather as a rasp than as a dart or spearhead. On each side is a number of acanthocysts, each with several accessory stylets.

The length of the proboscis is of no systematic importance, for in some of the longer forms, such as *Carinella*, *Lineus*, *Eupolia*, *Eunemertes*, it is very short; whereas, in other cases, either longer or shorter worms like *Cerebratulus* and *Amphiporus*, it may be actually longer than the body. The exact use of this pro-

[1] According to Montgomery (30), who follows Keferstein, they are complemental; he argues against the possibility of their transference and fixation in the funnel; his account of the structure of the sacs differs considerably from Burger's, for he describes an epithelium round each sac, which is a pouching of the wall of the proboscis cavity.

boscis of the Nemertines is uncertain. It appears probable that a poisonous fluid is discharged into the wound made by the armed proboscis—a fluid secreted by the epithelium of the hinder region of the proboscis. While in the Anopla the rods and nematocysts possibly have some stinging or numbing function.[1]

Eversion of the proboscis is effected by the contraction of the wall of the rhynchocoel, acting upon the contained fluid.

The rhynchocoel, which is developed as a cleft in the mesoblast that forms around the invaginating proboscis, is a closed,[2] cylindrical tube lying above the intestine; in *Drepanophorus*, alone, it gives rise to a series of long, narrow, non-muscular diverticula, right and left, which correspond in position with the intestinal diverticula (Fig XXI. *w'*). The wall of the rhynchocoel (or proboscis sheath) consists usually of an internal coat of longitudinal muscle, and an outer coat of circular muscles, some of which in *Carinella* are continued round the intestine. It is lined by a flat epithelium, which is replaced by goblet cells over the dorsal vessel, where this passes along its floor. The rhynchocoelic fluid contains flat, ellipsoid, amoeboid corpuscles, frequently coloured by red or yellow granules, possibly haemoglobin; as a rule, the cells are larger than the blood corpuscles, but vary in shape and size in different genera. It is noteworthy that even in a "resting condition," an attraction sphere is readily visible in them.

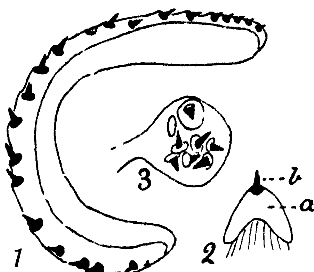


FIG XVII

The armature of the proboscis of *Drepanophorus crassus* (after Bürger) 1, the curved median acanthophore, with several stylets fixed upon it 2, a transverse section of it, *a*, basis of acanthophore, *b*, stylet 3, one of the numerous lateral acanthocysts

This characteristic apparatus has no exact counterpart in the Platyhelmia, although it resembles in its general anatomy and mode of action each one of the four "proboscides" of *Tetrarhynchus*, and still more, the complex rostellum of *Drepanidotaenia*. But with these it can have no genetic relation; the Nemertines have probably been descended from some Turbellarian-like ancestor, and among these the family Proboscidae appear to furnish a starting-

[1] It is worth noting that M'Intosh doubts both the fact that poison is secreted, and the fact that the organ is one of aggression. There are curiously few actual observations on the eversion of the proboscis The matter requires investigation, as also does the mode of action of the muscles of the organ C B. Wilson gives an account of the employment of the proboscis in burrowing and locomotion; see "Habits, etc., of Cerebratulus lactens" (in *Q J. M. Sci* xliii. 1900, p. 97), for many interesting facts concerning the habits of this species

[2] Burger speaks, with considerable hesitation, of communications with the vascular system in *Cerebratulus*.

point for this proboscis (see p. 17). Nevertheless, it is a very long step from the one to the other, and no intermediate stages are known; for in the Proboscidae there is nothing comparable to a rhynchocoel, which must have been developed *pari passu* with the elongation of the eversible organ—as the only means of everting the proboscis—probably in the same way in which it is developed ontogenetically. Burger has suggested that it represents the pharynx of the Turbellaria, and sees in those genera in which the rhynchostome is coincident with the mouth the original condition. But apart from the difficulty of comparing structurally the proboscis with the tubular pharynx, it is extremely improbable that the Metanemertini—in which alone this condition is realised—should have retained a primitive condition in this respect, whilst in the remainder of their anatomy they are so evidently much less primitive than the Proto- or Meso-nemertini, in which there is no sort of connection between the two organs.

The nervous system of the Nemertines (see 6, 16, 17) is primitively in the form of a network, as in Turbellaria; but in the lower orders this network retains a more superficial, and phylogenetically, more archaic position than in that Class; for in the Protonemertini it lies among the bases of the epidermal cells (*Carinina*), as in the Coelentera (Fig. XVIII. 1, *e*), in *Carinella* and *Hubrechtia* it sinks through the basement membrane so as to lie immediately below it, in the Mesonemertini this process continues, so that in *Carinoma* the nerves lie outside the circular muscles, in the region of the foregut, but come to occupy a deeper position, viz. in the longitudinal coat, in the posterior region of the body—a position which they occupy throughout the body in *Cephalothrix* (Fig. XVIII. 2). Finally, in the Metanemertini the nervous system has sunk into the parenchyma, and occupies the same position as in the Turbellaria (Fig. XVIII. 3) The case of the Heteronemertini must be considered apart, for although the nerve cords lie between the muscular coats, this position is not so much the result of sinking inwards, as of being thrust downwards by the development of a new muscular layer outside the circular coat (Fig. X); indeed, with regard to the latter, the nerves occupy the same position as in *Carinella*.

The nervous network, even in the lowest Nemertines, presents a differentiation into a central and peripheral system, though it is impossible to draw a hard-and-fast line between them; for certain tracts have, as in the Turbellaria, become larger and more definite than others, giving rise to longitudinal nerve stems; but of these only three are recognisable, namely, a pair of stout lateral stems, and a smaller median dorsal nerve. These traverse the whole length of the body, and are connected at each end by a transverse, supra-enteric commissure or anastomosis. The elongated

ring, thus formed, consists of nerve fibres wrapped round by ganglion cells. As in the case of all the Coelomocoela, except Echino-

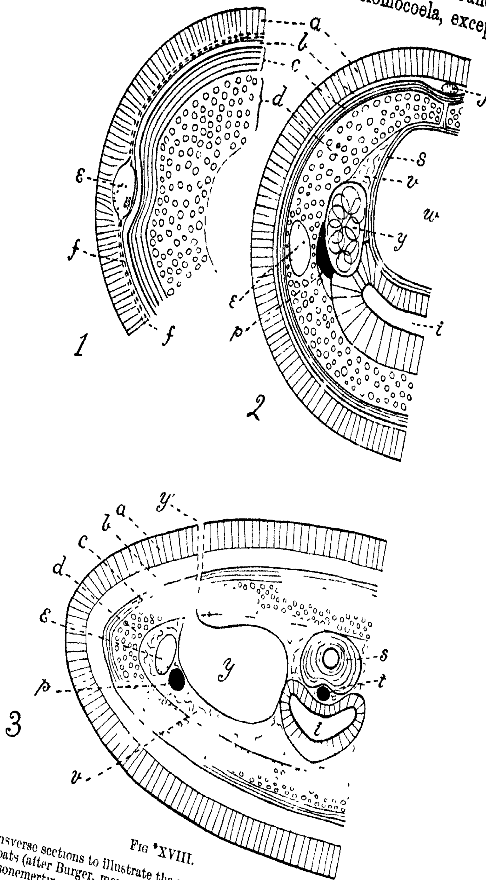


Fig. XVIII.

Portions of transverse sections to illustrate the position of the lateral nerve stem in relation to the muscular coats (after Bürger, more or less altered) 1, *Carinina*, a Protonemertine, 2, *Cephalothrix*, a Mesonemertine, 3, *Amphiporus*, a Metanemertine a, epidermis, b, basement tissue, c, circular muscles, d, longitudinal muscles, e, lateral nerve stem, f, peripheral nerve sheet, i, enteron, j, dorsal nerve, p, lateral blood-vessel, s, proboscis sheath or wall of the rhynchocoel, the proboscis is omitted, t, dorsal blood-vessel, v, parenchyma, w, rhynchocoel, y, gonad, y′, position of genital pore.

derms, the anterior end of the system has come to be of greater importance than the rest, here each lateral stem thickens to form a ganglion, to which is added a dorsal ganglion, closely connected

with it (Fig. XIX.). The two ganglia are developed from different "rudiments,"—the dorsal possibly represents the prostomial "cerebral ganglia" of the Annelids; the ventral probably represents the suboesophageal ganglion of an Annelid. But here in the Nemertines there is no repetition of ganglia; these two ganglia constitute the "brain," and are so closely united in the lower forms that in *Hubrechtia* there is no external demarcation between them. But usually they are distinct as a dorsal and ventral lobe of the brain. The dorsal lobe is usually the larger, and is connected with its fellow by a delicate, supra-proboscidial commissure; the ventral lobes are connected by a broader commissure below the proboscis tube. The "cerebral organ" frequently becomes very closely associated with the hinder part of the dorsal ganglion (Fig. XIX. *P*), or a special ganglion may separate from it, to become connected with the organ (Fig XX. *L*). The dorsal lobe is essentially sensory; the ventral motor.

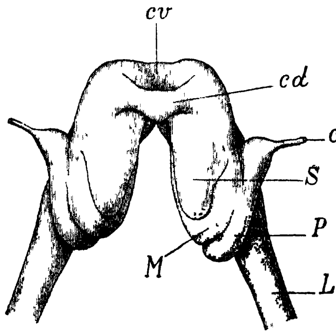


FIG XIX

Brain of *Eupolia giardii*, Hubr (from Perrier, after Hubrecht) *c*, aperture of cerebral organ, *cd*, dorsal commissure, *cv*, ventral commissure, *L*, lateral nerve trunk, *M*, middle lobe of the dorsal ganglion, *P*, posterior lobe (cerebral organ), *S*, dorsal ganglion

The third longitudinal cord is thin, and arises from the supra-proboscidial commissure, it always retains its superficial subepidermic position, even when the rest of the system has sunk into the parenchyma (Metanemertines). In all but these it gives off a branch which passes below the circular muscles, and runs back as a second dorsal nerve (see Figs VIII, X. *k*). Hubrecht, its discoverer, called it the "proboscidial-sheath nerve."[1] These three longitudinal nerves—specialisations as they are of a primitive network of cells and fibres—are connected by this network, or tunic, in the Protonemertini and Heteronemertini, in some of which, especially *Hubrechtia*, it attains a considerable thickness. Even in *Carinella* this primitive nerve plexus exhibits a tendency to form circular, commissural nerves, for the circular strands are more pronounced than the rest. In the Metanemertines this nerve tunic has become specialised, in connection no doubt with the sinking of the whole system, for it is represented by a ladder-like series of ventral commissures connecting the lateral stems (Fig. XX.), and by a series

[1] For a suggestion as to the importance of the dorsal nerve, as well as of the proboscis and its sheath of Nemertines, in the evolution of Vertebrata, see Hubrecht (18).

of nerves, passing dorsally from the latter, which subdivide and enter the muscular body wall. In the Mesonemertini nothing is known of a nerve tunic or its representative. In *Drepanophorus* the lateral stems appear to lie nearer the ventral mid-line than usual (Fig XXI.); this is due rather to the great development of the lateral margins of the body than to a real movement of the

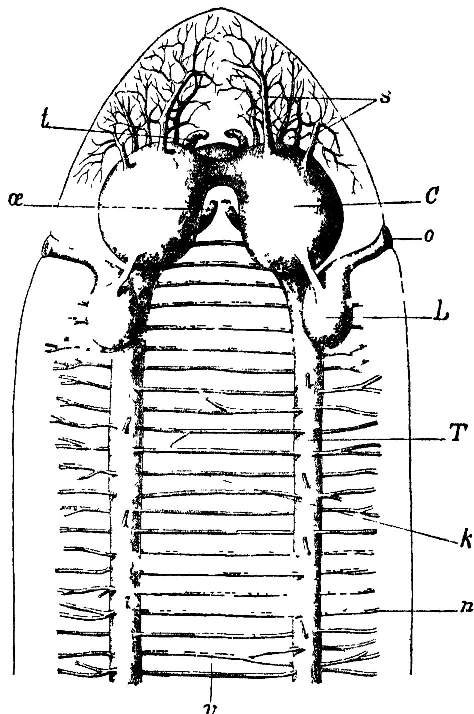


FIG XX

Nervous system of *Drepanophorus lankesteri*, Hubr (from Perrier, after Hubrecht) *C*, dorsal ganglionic lobe, *k*, transverse commissures between the lateral stems, *L*, hinder lobe of brain or cerebral organ, *n*, peripheral nerves, *o*, aperture of cerebral organ, *œ*, nerves to stomodaeum, *s*, sensory nerves to snout, *T*, lateral nerve trunk; *t*, nerves to proboscis, *v*, transverse commissures.

nerves, for they occupy the same position, relatively to the rhynchocoel and midgut, as in other forms. On the other hand, in *Langia* (Fig. XXII.), the upward growth of the lateral margins has evidently carried the lateral nerves upward, for they lie on the same horizontal plane as the rhynchocoel.

The nervous system of Heteronemertines is tinged by haemoglobin; the muscular tissue of *Euborlasia* is reddish, but whether this is due to the same pigment is unknown.

The most interesting and characteristic sense organ is the ciliated, neuro-glandular pit at the side of the head (see 5, 11).

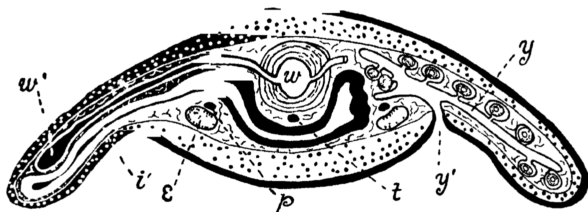


FIG. XXI

Transverse section of *Drepanophorus albolineatus*, Burg (after Burger), to show the apparent ventral shifting of the lateral nerve cord (*e*) due to the great development of the intestinal caeca (*i'*) and of the diverticula of the rhynchocoel (*w'*), *i*, intestine, *p*, lateral blood-vessel, *t*, dorsal vessel, *w*, rhynchocoel, *y*, gonad, *y'* genital pore

It presents various stages of elaboration, and is only absent in the Mesonemertini, and in such exceptional genera as *Malacobdella* and

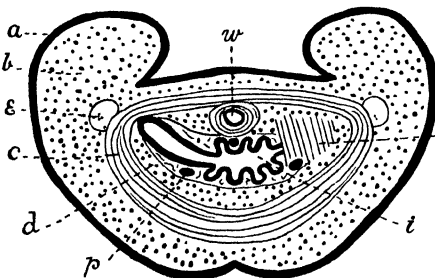


FIG XXII

Transverse (slightly oblique) section of *Langia formosa*, Hubrecht (after Burger) *a*, epidermis, *b*, longitudinal muscle of cutis, *c*, circular muscles, *d*, longitudinal muscles (inner coat), *e*, lateral nerve cord apparently shifted dorsalwards, *i*, intestine with caecum on left side, *p*, lateral blood-vessel, here shifted ventrally, *w*, rhynchocoel, *x*, dorso ventral muscles forming, a septum between successive intestinal caeca

Pelagonemertes. This organ, which is no doubt phylogenetically derived from the simple pit of some Turbellaria, becomes closely

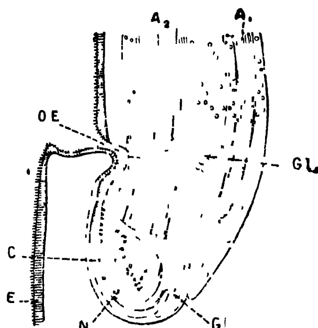


FIG. XXIII

Cerebral organ of *Cerebratulus* in schematic, longitudinal section (from Perrier, after Burger) A_1, A_2, nerve fibres in upper and lower part of dorsal ganglion, *C*, cerebral canal, *E*, epidermis, *Gl*, *Gl*, glands opening into the lateral canal (the posterior bunch is probably represented in *Drepanophorus* by the "glandular canal"), *N*, nervous tissue of the cerebral organ, *OE*, aperture of canal into the posterior end of the horizontal cephalic cleft

connected with a special ganglion, or in Heteronemertines penetrates the hinder part of the dorsal ganglion, of which it forms a definite

lobe; hence the organ receives the name "cerebral organ." In its simplest form, in the Protonemertini, it is a mere groove in the epidermis not extending deeper than the basement membrane; it is lined by ciliated cells, and at the bottom are large gland cells; the organ is supplied by nerves from the brain. In *Carinella rubicunda* and others the groove becomes an oblique canal, the blind end of which is surrounded by a mass of ganglion cells, lying outside the cutis. In the higher forms the canal penetrates deeper into the body as far as the brain (Fig XXIII.) The gland cells and the nerve tissue associate with it, increase in amount, and the canal becomes differentiated into two regions—an extra-ganglionic "lateral canal," and an intra-ganglionic "cerebral canal" (*C*), which frequently terminates in an enlarged sac. In *Drepanophorus* the cerebral canal is quite exceptional, in that it bifurcates—one branch terminating in a sac with sensory epithelium (Fig. XXIV *C*), the other being glandular (*GT*), this, in *D. crassus*, extends backwards beyond the brain as a free tube. In several genera of this order the cerebral organ lies in front of the brain, *e g. Tetrastemma*, sp of *Eunemertes* and of *Amphiporus*, in others it lies at the side, and in still others, behind the brain—in which case it attains a great size. In all cases the organ is separate from the brain, from which it receives nerves.

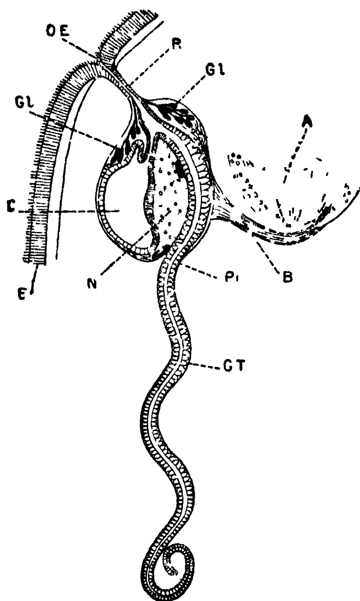


Fig XXIV.

Cerebral organ of *Drepanophorus crassus* (from Perrier, after Burger) Schematic horizontal section, *A*, hinder end of dorsal ganglion, *B*, nerve to cerebral organ, *C*, cerebral sac—the dilated outer limb of the original canal—embedded in a mass of nerve tissue, *E*, epidermis, *Gl*, glands opening into the lateral canal, *GT*, the glandular canal, projecting freely from the ganglion (in this species), *N*, nervous portion of the organ, *OE*, aperture of lateral canal of the organ, *P*, pigment, *R*, lateral canal

The lateral canal of the cerebral organ opens to the exterior in relation to a furrow or groove on the head, which is somewhat variously disposed in the class. It is simplest in the Protonemertini, being a shallow, vertical furrow—the "cephalic furrow,"—marking the head from the trunk (Fig. XXV.), and in most of these the cerebral organ is little else than a deeper part of the furrow, but in *C. rubicunda* opens independently of the latter. In Metanemertini and in the genus *Eupolia* this furrow becomes crescentic with its con-

vexity backwards, and the dorsal and ventral horns nearly meeting their fellows of the other side (XXV. *C*); the bottom of this furrow is subdivided into pits by tranverse ridges; the "lateral canal" opens at the hindmost part of the curve.

But in the Heteronemertini (Fig. XXV. *C*, *D*, *E*) this vertical

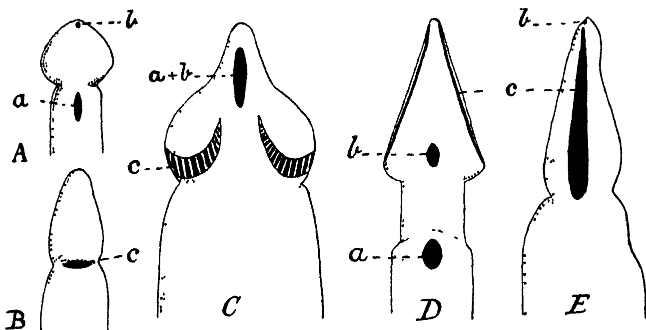


Fig XXV.

Heads of Nemertines (after Burger) *A*, ventral, and *B*, lateral views of *Carinella*, *C*, ventral view of *Drepanophorus*, *D*, ventral view of *Valencinia*, *E*, lateral view of *Cerebratulus*, *a*, mouth, *b*, rhynchostome, *c*, groove in side of head, vertical or horizontal, in connection with the cerebral organ

furrow is replaced by a horizontal "cleft"—deeper or shallower, longer or shorter—especially well developed in *Cerebratulus* (Fig. I. *g*), where it starts at the apex of the snout on each side, and is so deep as to touch the brain; at its hindmost point the "lateral canal" opens. The haemoglobinous nerve tissue is thus brought close to the surrounding medium, and on this account Hubrecht suggested that the cerebral organ is respiratory in function. Probably both the "cephalic furrow" (or cleft) and the cerebral organ together are derived from the "ciliated pit" of Turbellaria.

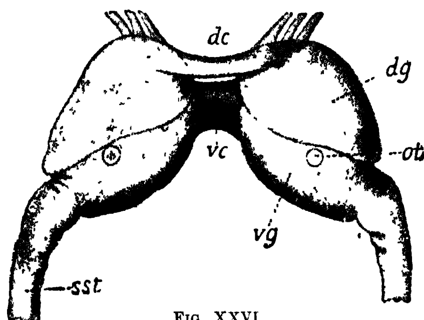


Fig XXVI

Brain of *Ototyphlonemertes* (from Joubin, after Burger). *dc*, dorsal commissure, *vc*, ventral commissure, *dg*, dorsal lobe or ganglion, *vg*, ventral, *ot*, otocyst, *sst*, lateral nerve trunk.

Eyes are present in many Nemertines, and have the structure of Polyclad eyes. An otocyst occurs only in *Ototyphlonemertes*, resting against the ventral ganglion, and resembles the molluscan otocyst (Fig. XXVI.).

At the anterior extremity of the snout, above the rhynchostome,

is a "frontal organ"—a single retractile papilla in Metanemertini and in *Eupolia;* or a group of three papillae in *Cerebratulus* and *Micrura*. In all cases the papilla consists of ciliated cells, between which there open the ducts of the "frontal gland" (cf. Acoela).

Finally, in *Carinella*, there is present a "lateral organ" in the form of a retractile papilla, close to the excretory pore on each side, and recalling that of Capitellids.

The vascular system (35) consists primarily of a pair of lateral vessels (in Proto- and Meso-nemertini) extending along the entire length of the worm, lying in the parenchyma, just above the level of the lateral nerve. Anteriorly these vessels pass through the nerve ring (Figs. II. *p.*, XXVII. *c*) and unite at the tip of the snout—and in *Carinella* are also joined at the level of the brain—at the posterior end they are united by a supra-enteric commissure. The anterior part of the lateral vessel in *Carinella* is dilated (*b*), and a series of short vessels are given off to a longitudinal, lateral, proboscis-sheath vessel. In the Metanemertini (Fig. XXVII. 2, *m*) a median dorsal vessel arises from this intra-neural commissure and passes backwards above the gut, to fall into the supra-anal commissure. For a part of its course the dorsal vessel runs just within the rhynchocoel, the epithelial lining of which is here modified. Moreover, a series of transverse vessels unite these three longitudinal ones, but no branches are given off by the system—no blindly ending vessels—except in *Malacobdella* (Fig. XIII.).

The Heteronemertini (and *Hubrechtia*) combine the three longitudinal and transverse vessels of the Metanemertini with the anterior dilated regions of the Protonemertini, from which several pharyngeal vessels arise (Figs III, XXVII 3, 4).

This system of vessels is entirely closed, and contains a colourless fluid in which there float nucleated cells of fixed outline, usually oval and flattened. In the majority these corpuscles are colourless, but in a few (*Amphiporus*) they are red or yellow; in others yellowish with a green tinge; and in *Euborlasia* they are yellow, spotted with red, so that the blood appears red. The yellow tint is due to haemoglobin

Details are wanting as to the way in which this "blood" or "haemal fluid" (?) circulates in those forms in which only the lateral vessels are present. According to Burger, the blood, in Metanemertines, flows out of the dorsal, through the circular vessels, into the lateral ones, returning to the dorsal vessel at each end of the worm. But this is very unsatisfactory and uncertain. As to the morphological nature of this vascular system, it seems certain that it is not "coelom" as we understand the term in the case of Annelids, etc.; it has none of the characters which we associate with this cavity. It arises in the young worm during the formation of the "imaginal discs," as a space or spaces

in the mesoblastic jelly ("mesenchyme"). Although Salensky terms this space "coelom," it is more probable that, if there is a coelom at this stage, it is represented by the narrow cleft between the somatic and splanchnic mesoblast, such as exists in some cases

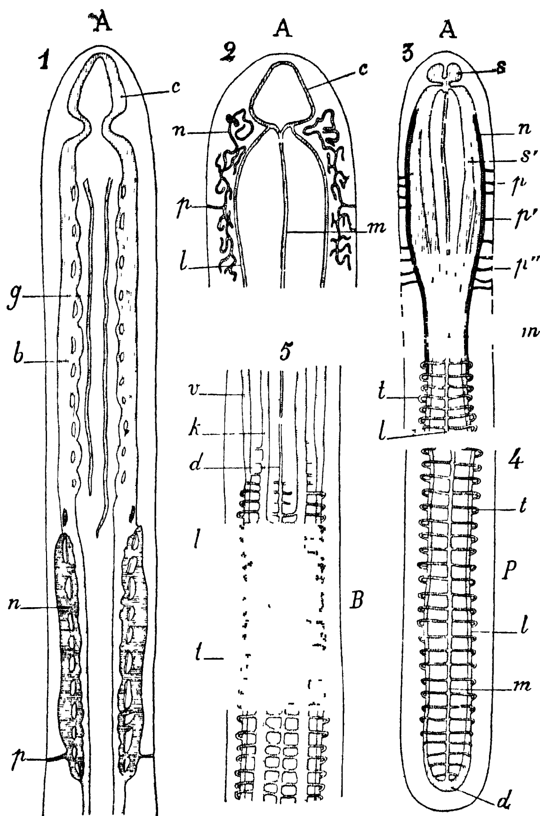


FIG XXVII

Plan of the vascular and excretory systems (from Perrier, after Oudemans) 1, *Carinella*, 2, *Drepanophorus*, 3, 4, *Eupolia*, 5, *Valencinia* (mid body) *c*, preoral anastomosis of lateral vessel (the intraneural anastomosis is not represented in 1), *d* (in 4), supra-anal anastomosis, (in 5) dorsal vessel, *b*, parastomodæal sinus, *g*, vessel of proboscis sheath, *k*, lateral vessel of proboscis sheath, *l*, lateral blood-vessel (in Fig 3 the index line is carried to the dorsal vessel, and in 5 to the proboscidial vessel), *m*, dorsal vessel, *n*, nephridium, *p*, *p'*, *p''*, nephridial pore or pores, *s*, preoral dilatation, *s'*, parastomodæal sinus, *t*, transverse vessels, from dorsal to lateral vessels, *v*, lateral vessel

according to Lebedinsky (26). The spaces run together to form a large sinus, which becomes divided into a right and left channel by the developing proboscis; these channels become the lateral vessels, and decrease in relative size. Probably this vascular

system is represented in the Turbellaria by the intercellular lacunae of the parenchyma.

It is by no means certain what function the system performs in Nemertines. It is so far removed from the surface of the body and the surrounding medium, except in those cases in which the cerebral organ impinges upon the lateral vessel, that respiration seems out of the question. Even in the head, where the vessels are dilated into capacious sinuses, these are below the musculature of the body wall, except in the region of the mouth (*Cerebratulus*, etc.), where they come up to the basement tissue; but in this case it has no respiratory pigment as far as we know. Even if there is a certain amount of gaseous interchange in this region it seems more probable that the "vascular system" in the Nemertines serves rather as a "nutritive" (lymphatic) system, for the vessels are placed close to the wall of the enteron, and dissolved food material can readily diffuse into them. Further, the excretory system is always in contact with the lateral vessel, from which the excretory products are, no doubt, removed. It is probable that the distension of the dilated vessels at the anterior end serve also to give firmness to the head during burrowing.

The excretory system, which was originally observed by Max Schultze and figured by him,[1] is always paired, and usually of limited extent, being confined to the region of the foregut (Fig. XXVII. *n*), extending backwards in short species at the side of the enteron; and, in *Lineus lacteus*, forwards beyond the mouth.[2] The system (see 35) consists essentially of a longitudinal, horizontal canal, which opens externally below the lateral nerve, through a short, transverse duct (*p*). This is usually single, but in *Amphiporus*, *Valencinia longirostris*, and *Eupolia curta* (Fig. XXVII. 3) there is a number of ducts, one behind the other, each opening by a pore. The canal which is lined by a ciliated epithelium runs alongside the lateral vessel, and gives origin to a number of branches, generally of the same diameter as itself. These are short in Protonemertini, or longer in other cases, and may even be branched in Metanemertini, where they are wrapped round the blood-vessel. Each branch terminates in a multicellular dilatation, containing a "flame" (Fig. XXVIII). These "end bulbs" push the wall of the blood-vessel inwards; but there is no

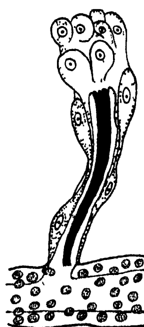


FIG XXVIII.
A "flame cell" (altered after Burger)

[1] Max Schultze, *Beit. z Naturgesch d. Turbellarien*, 1851.

[2] Montgomery has recently described a series of nephridia extending throughout the length of the body in *Stichostemma*, each with from one to five ducts.—*Zool. Jahrb.* (*Anat.*), x. 1897, p. 265.

communication between the two systems, as Oudemann believed. There is never any anastomosis between the branches, nor any communication between the right and left organ.

The restriction of the system to a limited region of the body, and the absence of a network, such as occurs in Platyhelmia, is no doubt connected with the existence in the Nemertines of a "vascular or lymphatic system," which brings to the excretory system the material for its activity. There can be no doubt but that the system, though differing in details and in plan from that of Platyhelmia, is descended from it, and belongs to the same category as the "head kidney" of Annelids, which it resembles in its limitation to the stomodæal region of the gut.

The reproductive organs contrast as much as is possible with those of the Platyhelmia, for in the Nemertines there is nothing resembling the copulatory organs of the former phylum; there are no glands set aside for the formation of egg-cases, no differentiation of the ovary into "germarium" and "vitellarium." We have to do with mere sacs (Fig XVIII. *y*) containing the products of the proliferation and modification of the epithelial cells which line these sacs, and in due time, when these products are ripe, these sacs push their way outwards through the body-wall to form genital ducts, which will ultimately open to the exterior In a few Metanemertini ovaries and testes occur together and ripen simultaneously (*Prosadenoporus*, two sp., *Tetrastemma*, two sp., *Geonemertes* spp., and *Prosorochmus*), while "*Borlasia*" *Kefersteini*, *Stichostemma Eilhardi* are protandric hermaphrodites.

The genital sacs are coextensive with the midgut, and as a rule are repeated in a regular series, one sac between every two successive enteric pouches. This regularity is, however, concealed in *Amphiporus*, in that only some of them ripen at a time, so that in *A. pulcher* there are only five, at irregular distances In *Carinella* and *Malacobdella*, in which the intestinal pouches are not found, the genital sacs are closely packed together. The pores, as a rule, form a simple linear series above the lateral nerve, but in the two genera just named, and in *G. australiensis* they form a broad band extending nearly to the mid-dorsal line. In *Drepanophorus*, owing probably to the great development of the dorsal organs of the body, *e.g.* the rhynchocoel, the genital organs, like the lateral vessels, seem to be ventral (Fig. XXI.).

The genital sacs arise either (*a*) simultaneously with the developing genital cells (as *Carinella*, *Malacobdella*, *Prosadenoporus*, and others) from a group of parenchymal cells which gradually become differentiated into a central mass of "germ cells" and a peripheral membrane of flat wall cells; or (*b*) the sacs develop first, and then from some of the epithelial cells the germ cells arise (as in *Cerebratulus*, *Drepanophorus*) by the accumulation of yolk spherules

around the nucleus, etc.; in these cases the sac seems empty when the worm is mature, for the ripe egg cells push the wall outwards, and come to lie in independent follicles in the parenchyma (Fig. XXI.).

It has been pointed out by Hatschek and by Mayer that each genital sac presents all the usual relations and characters of a coelom, and these sacs are the only organs which can be regarded as such. The excretory system, at one time identified as coelom, is now known to be epiblastic in origin (as in other worms) and to appear after the mesoblast has formed, nor has the vascular system any claim, from developmental considerations, to the title. The fact that the genital sacs appear late, and in the simplest forms arise contemporaneously with the genital cells (as they do also in Platyhelmia), cannot be regarded as a solid argument against the view. It is, indeed, rather remarkable that in both these groups, the lowest of the Coelomocoela, the coelom is an inconspicuous cavity. We are so generally led to think that the coelom is a constant accompaniment of the mesoblast, that we forget that possibly the chamber is later, phylogenetically, than its wall. Here, in Nemertines when the gonads are mature, there is a remarkable resemblance, in their repetition, in their relations to other structures, to the coelomic segments of Annelids.

The matter of "metamerism" is closely bound up with that of the coelom. In the Annelids it is the mesoblast and its cavity that first present repetition during embryogeny; the internal segmentation which exists in the Nemertines—the repetition of the gonads, of the intestinal pouches, of the blood-vessels and nerves, and in *Drepanophorus* of the rhynchocoelic diverticula—is essentially the same as in Annelids. But in the Nemertines it is never accompanied by external marks of metamerism, with the interesting and important exception of the genital pores. There is no constriction of the body, no interruption in the musculature of the body wall

It is a remarkable fact that the nephridia are not metamerically repeated; it is true that in *Amphiporus* and in *Valencinia* the nephridial ducts and pores are numerous, but this repetition is quite irregular, asymmetrical, and not coincident with that of other organs. This may perhaps be explained by regarding the nephridia of Nemertines as homologous with the "head kidneys" of Annelids, which appear early in ontogeny and differ in structure from the metameric nephridia. We must believe that these have not yet made their appearance, phylogenetically, in the Nemertines. This fact is strongly opposed to Perrier's view that this group is a degenerate descendant from Annelids, for we should then expect to find traces of nephridia in the "trunk," where the gonads, etc., are situated. The more usual view, that they are descended from the Turbellarian stock, and have in some respects, and in some degree, followed the Annelid line of evolution, is the more plausible view. The condition of the nervous system fits in with this view—specialisation of two lateral tracts, which in the higher Annelids are destined to come together and even to fuse on the ventral surface.

The statement of Lebedinsky, too, that the mesoblast arises from two

pairs of cells, each of which gives rise to a "mesoblastic streak," destined to split into a somatic and splanchnic coat, with a small coelom between, is a further support for this view.

Reproduction and Regeneration.—The best known ontogeny is that of the Pilidium (see above) of the Heteronemertines, and of the larva of Desor, which occurs in the life-history of *Lineus gesserensis* (1, 19).

Internal fertilisation has been definitely observed by Dendy in *Geon. australiensis* (10). It occurs also in the viviparous forms, such as *Prosorhocmus claparedii*, etc.

The Metanemertini have been most studied; they undergo no metamorphosis, their development is direct, and has recently been studied in several genera by Lebedinsky (26). Nothing is known about the history in Protonemertini, nor *Eupolia*, and very little in Mesonemertines, but so far as we know it is direct (9). But in addition to this sexual generation, a kind of asexual reproduction exists in the larger species, which, as is well known, break in pieces when attacked, or possibly automatically. Dalyell was the first to recognise that *Lineus* was able to regenerate a new posterior end M'Intosh found that the hinder pieces could reproduce a new "head" and proboscis as well as a new tail. Brown (4) has recently made a study of the same species. Burger has investigated the regeneration of the proboscis in *Drepanophorus*, and Benham (2) has traced some of the histological conditions of a "fragmenting" *Carinella*, and has suggested that fragmentation may take place, apparently, without any stimulus other than the ripening of the gonads, which are present in this case, only in the "segmented" hinder region of the worm Hubrecht saw in this power of fragmentation a precursor of metamerism, and there can be little doubt but that this power of separating into pieces, even automatically, is of considerable value to the worm, for the part, overburdened with genital products, must be less able to help in the movement of the worm, and thus hinder its escape from enemies, or search for food. If each piece had the power of reproducing a head, after expulsion of the genital cells, there would be a close analogy with the asexual reproduction of Syllids and other Annelids.

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ADDENDA AND CORRIGENDA TO THE NEMERTINI

THE following notes have kindly been furnished by Mr R C Punnett of St Andrews In a rapidly growing study like that of important groups of marine organisms, it is impossible for an author who has removed to so distant a colony as New Zealand, where Dr. Benham now is, to give the final touches to his work, if it is to be up to date. The editor has gladly availed himself of Mr. Punnett's knowledge of the Nemertines to complete this chapter E R L

9th *July* 1901.

Within the last few years considerable attention has been paid to this group of worms, resulting in the discovery of certain points in the anatomy of the group, and also in the addition of a number of new forms to those already known This has led to the establishment of the following new genera —CARINELLIDAE, *Callinera*, Bergendal, *Carinesta*, Punnett, (FAM ?) *Gononemertes*, Bergendal. EUNEMERTIDAE, *Paranemertes*, Coe, EUPOLIIDAE, *Parapolia*, Coe, *Zygeupolia*, Thompson, *Oxypolia*, Punnett, LINEIDAE, *Micrella*, Punnett, *Lineopsis*, Staub Of these the two genera *Zygeupolia* and *Micrella* are of especial interest on account of certain primitive features which they exhibit, and which render them of importance in the question of the derivation of the two great Heteronemertean families. Among the more interesting points which have been recently noted in the anatomy of the group may be mentioned the following —

Montgomery (vi) has carefully described and classified the various connective tissues in the group In the same paper he has come to the conclusion that a body cavity is sometimes represented by spaces between the alimentary canal and inner longitudinal muscle layer of the Heteronemerteans. Montgomery has also pointed out that whilst the posterior nerve commissure is almost always above the anus in the Metanemerteans, in the genus *Proneurotes* it is sub-anal. It has also been shown (vii) that this commissure in the genus *Eupolia* may be either above or below the anus, or may be altogether absent. The excretory system has been worked out in numerous forms ((iii), (iv), (vii), (viii), (ix), (xi)), and in one species of *Eupolia* it has been shown to possess both ducts opening to the exterior, and also ducts opening into the alimentary canal (vii) It may be further noted that the caudal appendage of the Lineidae, upon which much stress is laid in classification, shows differences of structure which may ultimately necessitate a

revision of the family in which it is found (ix). Contributions to the development have been made by Coe (ii) and Wilson (xii).

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(xii) *Wilson.* (Habits and Development) Quart. Journ. Mic. Sc. vol. xliii. 1900.

P 163 (α). Mention should be made of the oesophageal (or buccal) nerves which occur throughout the group

(β). In spite of what has been often written to the contrary it is exceedingly probable that in most cases, if not all, the blood-vessels are destitute of muscle fibrils, and that the blood is kept in circulation by the waves of contraction passing over the body wall.

(γ). The transverse connections are always dorsal to the gut.

(δ). The gonads may open on the ventral surface within the area between the lateral nerve cords

P 168 (α). Hubrecht states that in *Lineus gesserensis* the excretory system arises as an out-pouching from the endodermal portion of the alimentary canal.

P. 173 (α) *Drepanophorus* is characteristically tropical and sub-tropical. *Cerebratulus* is just as much tropical and temperate as arctic.

P 173 (α). The "tail" differs in structure. The alimentary canal does not necessarily extend into it.

P. 176 (α) The "retractor" end of the proboscis is not always attached.

P. 178 (α). The largest number of stylet sacs yet met with in an *Amphiporus* is twelve.

P. 182 (α) The median dorsal nerve cord in the Heteronemerteans is situated below the cutis and outer longitudinal muscle layer.

P. 187 (α). "Head gland" is the term more frequently used here (=Germ. *Kopfdruse*).

P. 189. The great majority of the species of *Amphiporus* possess only one pair of excretory ducts.

INDEX

To names of Classes, Orders, Sub-Orders, Families, and Genera; to technical terms; and to the names of Authors discussed in the text.

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